A STUDY OF THE PHYTOSAURS

WITH DESCRIPTION OF NEW MATERIAL FROM WESTERN NORTH AMERICA

BY

CHARLES L. CAMP

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FOREWORD

During the past eight years the Museum of Paleontology at the University of California has included in its program the collection and study of fossil remains from continental Triassic deposits of the southwestern states. One object of this work has been to ascertain the relationships of the faunas to those of Europe and to make some progress in the paleontological correlations of various more or less isolated Triassic formations in America.

As the collections accumulated it became apparent that a concentration of effort in one area might provide an adequate series of specimens from a sequence of horizons in a single geological formation. The rarity of such favorable conditions for the observation of a chronological sequence of forms made it seem desirable to continue this phase of the study during several field seasons. During the preparation of the material it was also found possible to increase our knowledge of the structure and probable relationships of some of the forms.

The present report accordingly deals with a series of "species" of phytosaurian reptiles from a number of stratigraphic horizons in the Chinle Triassic, with comparisons between these forms and forms previously described, and with the structure of the phytosaur skeleton. Newly available data that may be used in helping to solve the vexed question of the correlation of the American Mesozoic "Red Beds," have been outlined here and will be more completely reviewed as subsequent reports appear. Opportunity has also been taken to present a tentative classification and phylogeny of the phytosaurs, with a discussion of their relationships.

The entire project, of which this report is a beginning, has received the generous support of Miss Annie M. Alexander, the founder and patron of the Museum of Paleontology in this University. Miss Alexander and Miss Louise Kellogg, indeed, instigated this work through their own pioneer explorations in the field.

The following persons, and many others, have by advice or assistance contributed to this paper:

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For loan of material I am indebted to Dr. J. E. Hyde, of Western Reserve University; Dr. C. W. Gilmore, of the United States National Museum, and Mr. Dick Grigsby, of Adamana, Arizona.

CHARLES L. CAMP.

UNIVERSITY OF CALIFORNIA,
March 8, 1929.

GENERAL REMARKS

The phytosaurs are a group of extinct, carnivorous reptiles superficially resembling the crocodiles and gharials. They occupied the same kinds of habitats in the Triassic world as the Crocodilia do in the present. They were similar to the Crocodilia in bodily form, in habits, doubtless also in their adaptive radiation and in their wide distribution, and they became extinct just before the Crocodilia emerged, having left a fossil record only in the Triassic.

The Phytosauria are placed with the dinosaurs, pterodactyls, and aëtosaurs having in common with these a fenestra in front of the eye for accommodation of the anterior pterygoid muscles. They have been considered as ancestral to the Crocodilia by Huxley, but this has been denied by some who conclude that certain features in their structure remove them from the direct line of ancestry of crocodilians.

Superficially they resemble most closely the gharials (*Gavialis* and *Tomistoma*) but they differ from these and all other modern crocodilians in the structure of the snout, the open palate, the small size of the palatine fenestræ, the presence of an antorbital fenestra, the structure of the brain case, the shoulder girdle and pelvis, the form of the carpus, and the amphicœlous character of their vertebræ. The extended snout consists chiefly of the premaxillary bones, and the external nares are on top of the head whereas in crocodilians the snout is terminal. This fundamental difference would seem to remove the phytosaurs from a place in the direct line of descent of the crocodilians.

The phytosauroids now known from western America include small short-headed forms, the Stagonolepidæ, with a highly developed, shingle-like coat of armor; aberrant groups, the Desmatosuchidæ and the genus *Typothorax,* which have developed this armature in peculiar ways; medium sized, slender-snouted, presumably fish-eating genera, *Promystriosuchus, Mystriosuchus,* and *Rutiodon;* and more heavily snouted genera *Leptosuchus, Phytosaurus,* and *Machaeroprosopus.* The latter includes some gigantic species with specialized dentition, which possibly preyed upon smaller reptiles and amphibians and which are the largest phytosaurs so far discovered.

The structural differences between the various phytosaur genera are great considering the supposedly brief geological period in which the remains are found. There is also evidence for the view that some of these genera were of widespread distribution. For these reasons it is presumed that the employment of phytosaur remains in stratigraphic correlation will be of increasing importance as the faunas become better known.

The material at our disposal affords opportunity for review of a number of interesting questions. In the first place, the finding of numbers of skulls in the same stratigraphic horizons furnishes material for determination of individual, age, sex, and specific variation. Applying these data it is found that constant differences in structure at various stratigraphic levels may be observed. The geological and morphological evidence is believed sufficient to support our view that some of these differences in skull structure represent sequential change, or evolution from species to species within a single genus.

Secondly, we are enabled to compare more fully the western American species represented in our collections and the eastern American and old-world forms of which skeletal material is known. Further contributions are also made toward a knowledge of the structure and habits of the phytosaurs of the Chinle Triassic, and the environmental conditions of that period.

In reviewing the geological results of field work in the Southwest, it may be noted that our attempt to establish a more exact correlation of the subdivisions of the American and European Triassic is opposed to the advice of Branson and Mehl (1928). These investigators deem it inadvisable to employ Triassic vertebrates at the present time in stratigraphic correlation, even over local areas. Consideration should be given to the view that a form having many primitive characters may, owing to peculiarities of distribution or of preservation, actually occur in younger beds than a more specialized form. Nevertheless I believe that present materials warrant a further statement on the question of correlations.

GEOLOGY AND OCCURRENCES

Triassic Formations in the Southwest

Stratigraphic studies in the Painted Desert area and adjoining regions have resulted in the recognition, by most latter-day geologists, of three periods of Triassic sedimentation: the Moenkopi (Mo′-en-ko-py), the Shinarump (Shin-ar′-ump), and the Chinle (Chin′-lee). Early explorations by Whipple and Marcou, Ives and Newberry, Powell, Dutton, Ward (1901; 1905), Cross (1908), and Darton (1910) have been followed by the more detailed work of H. E. Gregory (1913, 1914, 1916, and 1917), Lee (1918), Shimer (1919), Butler (1920), Longwell (1921), Reeside and Bassler (1921), Darton in cooperation with the geologists of the Arizona Bureau of Mines (1925), Baker, Dobbin, McKnight and Reeside (1927), Prommel and Crum (1927), Branson (1927), and others.

The *Moenkopi* is now regarded as of lower Triassic age and, at least in part, of marine origin. These references are based upon determinations of invertebrate faunas (Reeside and Bassler, 1921, p. 67, and Baker, *et. al.*, 1927, p. 797).

We have collected plant remains in the "Moenkopi" at St. Johns, Arizona, but these have not been carefully identified. They consist for the most part of cycad leaves and *Equisetum*-like stems. Vertebrate and invertebrate tracks have also been taken from this formation at Flagstaff, Arizona, and in the Muddy Mountains of southern Nevada. No vertebrate bones have been discovered with the exception of the very dubious occurrence of an amphibian interclavicle at Tucker Springs, Arizona (see p. 12), and the discovery of bone fragments in a partial section of the "Moenkopi" made two miles east of Holbrook, Arizona (Gregory, 1917, p. 27). It seems probable that the bone-bearing conglomerate near the top of Gregory's section is a part of the so-called Shinarump.

The Moenkopi is separated from overlying formations at some points by great erosional unconformities and truncated local uplifts such as the one occurring three miles east of St. Johns, Arizona. The lower members of these overlying beds are, for the most part, conglomeratic and sandy and have been grouped together as the *Shinarump* formation. However, there are breaks in the continuity of the Shinarump, especially in the southeastern portion of its extent, and there are many conglomeratic lenses higher up within the overlying Chinle which contain the characteristic pebbles of the Shinarump. The fossils so far obtained in the pebble beds have been too fragmentary to be of use in separating the Shinarump and the Chinle. There are, so far as known, no widespread unconformities and since the lithologic criteria break down it would doubtless be preferable to discard the Shinarump as the name of a formation and to emphasize its true character—a basal conglomerate of the Chinle. To avoid confusion however the formational names used here conform with those adopted by the United States Geological Survey.

The Moenkopi underlies the Chinle throughout eastern Utah but has not been recognized in northern New Mexico. In the latter region the lower beds in the Chinle have not been successfully differentiated from the upper portion of the land-laid Abo formation which contains Permian fossils (cf. Huene, 1911*c*). Here what Huene calls the Poleo sandstone lies in erosional unconformity with the Upper Chinle (10 miles S of Canjilon). Huene has found Triassic fossils in and below the Poleo and correlates it with the Shinarump. Darton however considers it to be Permian. I should tentatively assign the Poleo and a part of the underlying shale beds to the Lower Chinle but the evidence is by no means conclusive.

In Texas the Triassic Dockum series rests without stratigraphic break upon the Permo-Carboniferous. The beds between the Triassic and Permian fossiliferous horizons are barren just as in New Mexico. A small portion of the Dockum fauna is similar to the Lower Chinle. The greater part of it is distinct, and doubtless more primitive.

The *Chinle* beds constitute a large part of the most extensive continental Triassic exposures in North America, if not in the world. They outcrop around the margin of the so-called Painted Desert of northeastern Arizona and extend into southern and eastern Utah, northwestern Arizona, and locally into southern Nevada.

In the southern portion of its extent the Chinle attains a thickness of over a thousand feet. In eastern Utah and northern New Mexico it diminishes to from 750 to 350 feet in thickness and in Nevada it is stated to have a thickness of from 500 to 3000 feet. Throughout its extent it is of terrestrial, mainly of fluvatile, origin and it is difficult to recognize minor subdivisions and members over any large area. It is of some importance to know whether the thicker beds in northeastern Arizona represent the same time interval of deposition as the thinner portions of the formation.

So far as the lithologic and paleontologic evidence goes it indicates, I believe, that approximately the lower 600–700 feet of sediments in northeastern Arizona were laid down prior to the deposition of the entire series in Utah. The upper beds in Arizona are similar to the northern series in their lithology and in their relations to the overlying Wingate sandstone. There is no sharp break however between the lower beds and the upper.

The lower beds, which I shall henceforth designate as the *Lower Chinle*, are characterized by great deposits of bentonite,[1] while this material is absent in the upper beds or so mixed with sand as to obscure its character.

[1] Determinations of this material have kindly been made by Dr. Victor T. Allen, formerly of the Department of Geology of this University, now of Department of Geophysics, St. Louis University, on samples taken in the Lower Chinle near Adamana (1923) and at Tanner Crossing (1927). His report upon a sample taken in the bone quarry (loc. 2078, specimen 27093 Univ. Calif. Dept. Pal.) in the lower fossil horizon at the Blue Forest, near Adamana, is as follows: "The material is Bentonite of which the chief constituent is montmorillonite. The index of refraction is determined as 1.526± .005, 2 v=20°–30°, optical character negative. Other minerals present are: anorthoclase, quartz, biotite. The texture of the material is schistose, with a soapy feel on fresh smooth surfaces. Well defined shards are lacking but the mineral composition indicates a derivation from rhyolitic ash."

Dr. Allen makes a further more detailed report upon the Chinle bentonite in *Amer. Journ. Sci.* (5), vol. 19, 283–288.

The Lower Chinle is further characterized by the more varied colors of its constituent lenses of bentonitic clays. These are more frequently gray, bluish, violet, red, and purple in color. The red bands are less extensive than in the Upper Chinle where the predominant color is red. The upper beds are characterized in places by thin projecting layers of hard, mortar-like, limestone containing chert nodules. Such layers are absent in the Lower Chinle.

Gregory (1917, p. 42) has tentatively distinguished four subdivisions of the Chinle in Arizona. The upper two of these (A and B) correspond to what I call here the Upper Chinle, the lower two (C and D) constitute the Lower Chinle.

Our collections from the Upper Chinle in Utah and New Mexico have not yet been prepared for study but enough is now known of their occurrence to warrant a general statement of certain paleontological differences between the Upper and Lower Chinle:

Upper Chinle	Lower Chinle
Machaeroprosopus, absent.	*Machaeroprosopus*, abundant.
Typothorax, locally abundant.	*Typothorax*, rare.
Amphibians, rarely found.	Amphibians, abundant.
Fossil logs, rare.	Fossil logs, locally abundant.

It may be added that the phytosaurian genus *Typothorax* has not been found in the lowermost levels of the Lower Chinle and that Amphibian remains are more common near the base of the Lower Chinle than toward the top.

There is evidence therefore of a gradual faunal and floral change in the beds, and an exact boundary between the two series usually cannot be ascertained.

The entire original thickness of the Chinle is not represented in the southern Painted Desert region in Arizona. The formation furnishes a large part of the present erosional surface or is capped locally by Tertiary lavas. Throughout most of the rest of its extent, however, the Upper Chinle is overlain by a massive, cross-bedded sandstone called the Wingate. This formation is one of the most striking features in the topography of the southwest. It extends in vertical red and white cliffs from the region of southern Nevada through central and southern Utah into northern Arizona and northeastern New Mexico. It forms the base of the Vermilion cliffs, Echo cliffs, a part of the walls of Glen Canyon, Indian Valley, and the canyon of the Grand River above Moab; also the extensive Comb Ridge and the summit of the Elk Ridge at the Bear's Ears in southeastern Utah.

The Wingate rests upon angular and erosional unconformities in the Chinle in the vicinity of Moab, Utah, and south of Canjilon, New Mexico. At other points it appears to be conformable or to lie in erosional unconformities only. In the region of Round Rock, in the Chinle Valley of northern Arizona, the Chinle appears to grade into the Wingate without a definable line of contact.

All this must mean that a portion of the Upper Chinle in the northern and eastern districts was lost by erosion before being covered, consequently any attempt to correlate fossil horizons in the Upper Chinle in these regions by measurement down from the base of the Wingate would be subject to error.

The only fossils reported from the Wingate are a few dinosaur tracks (Longwell, *et al.*, 1923, p. 13) which have not been identified. Consequently the age of the formation remains somewhat doubtful with the strong probability that it is Jurassic.

Age of the Chinle Formation

The Chinle has usually been assigned to the Upper Triassic. These determinations have been based upon the alleged similarity of the known vertebrates to those of the European Keuper, and the presence of supposedly Upper Triassic species of Ostracod crustaceans (Cross, 1908). Three species of shells of the genus *Unio* have been identified but as there is little variation in that form until the Cretaceous, they prove little except the presence of fresh-water conditions (Reeside, MS, 1927).

Huene (1922*a*, *b*; 1926) has lately attempted new correlations of the American terrestrial Triassic formations with those of Europe; basing his findings largely upon the vertebrate faunas. He recognizes both Middle and Upper Triassic faunas distributed as follows:

PROBABLY MIDDLE TRIASSIC

Wyoming, Popo Agie beds near Lander.
Colorado, various localities some of which are in the lower part of the Dolores formation.
Utah, two widely separated localities [in the Upper Chinle].
Arizona, various localities [in the Lower Chinle].
New Mexico, various localities, some of them definitely in and below the Poleo sandstone.
Texas, a portion of the Dockum formation.

UPPER TRIASSIC

New Mexico, localities [in the Upper Chinle] above the Poleo sandstone.

UNCERTAIN BUT "THOUGHT TO BE UPPER TRIASSIC"

Arizona, a portion of the fauna from near Tanner Crossing [Upper Chinle?].
Texas, a portion of the fauna from the Dockum.

Huene's correlations are not accepted by the American geologists Branson (1927) and Branson and Mehl (1928) who have commented at length upon the "uselessness of the fossils that have been described in making close correlations between the various areas" of Triassic sedimentation in the West.

While I recognize certain errors in Huene's tables, I believe that his findings agree fairly well with present paleontologic evidence. I shall therefore submit the following data (table 1) in a tentative modification of Huene's scheme made on the basis of new material in our collections from the Chinle of Arizona, Utah, and New Mexico.

I differ from Huene in restoring both the Lower and Upper Chinle faunas to the Upper Triassic. I tentatively regard the northern New Mexican Triassic as representing the Upper and possibly a part of the Lower Chinle; but I am not yet ready for a final word here.

Evidence for the Upper Triassic age of the entire Chinle is afforded by the presence of a *Stagonolepis* fauna in the lowermost beds of the Lower Chinle in Arizona.

TABLE 1

TENTATIVE REVISION OF HUENE'S CORRELATION OF THE AMERICAN AND EUROPEAN TRIASSIC FORMATIONS

Europe				Western America		Eastern America			
	Rhaetic		*Angistorhinopsis*			Newark	Connecticut	*Stegomus longipes* *Anchisaurus* *Omosaurus* *Podokesaurus*	Upper series
Upper Triassic	Keuper	Stubensandstein	*Mystriosuchus* *Phytosaurus* *Aëtosaurus*	Upper Chinle (Utah and northern New Mexico)	*Typothorax* (common) *Heterodontosuchus* *Coelophysis* *Episcoposaurus*				
		Lower	*Metoposaurus*	Lower Chinle (Arizona and western New Mexico)	*Metoposaurus* *Thecodontosaurus* *Placerias* (rare) *Typothorax* (rare) *"Stagonolepis"* *Machaeroprosopus*			*Stegomus arcuatus* *Clepsysaurus ? validus*	Lower series
	Lettenkohle		*Stagonolepis*				New Jersey and Pennsylvania	*?Eupelor* *Thecodontosaurus* *Clepsysaurus* (very similar to, perhaps identical with, *Machaeroprosopus*)	
Middle Triassic	Muschelkalk	Upper		Dockum (Texas and eastern New Mexico)	*Machaeroprosopus* (rare) *Buettneria* *"Coelophysis"* *Promystriosuchus* *Desmatosuchus* *Leptosuchus*		Virginia and N. Carolina	*Dictyocephalus* *Rutiodon carolinensis*	
		Middle		Popo Agie (Wyoming)	*Anaschisma* *Palaeorhinus* *Angistorhinus* *Dolichobrachium* *Brachybrachium*				
		Lower							
Lower Triassic	Buntstandstein	Upper							
		Middle	*Mesorhinus*						
		Lower							

There are no phytosaurs in either the Chinle or the Dockum which are as primitive as the genus *Paleorhinus* from the Chugwater (Popo Agie) of Wyoming. Neither is there any good evidence for the presence of *Angistorhinus* from the Chinle. The probable presence of Cotylosaurs in the Popo Agie is also indicative of an earlier age for the Popo Agie.

I hesitate to correlate the Dockum directly with the Chinle or the Popo Agie because of the differences in its fauna. Some of its phytosaurs, *Leptosuchus* and *Promystriosuchus*, are definitely more primitive than any from the Chinle; *Beuttneria* and *Machaeroprosopus* (?) *doughtyi* and *andersoni* are similar to *Metoposaurus* and *Machaeroprosopus* from the Lower Chinle. Doubts may be cast upon the supposed occurrence of *Typothorax* and *Episcoposaurus* in the Dockum. Case has not recorded them and it is possible that Cope had dermal plates of Case's *Desmatosuchus*.

The Dockum probably contains a number of horizons which have not yet been distinguished and it may be that certain of its levels are contemporaneous with the Lower Chinle while others are not.

The lower Newark series in Pennsylvania is similar in its fauna to the Lower Chinle, more similar apparently than are other known western beds. *Clepsysaurus* is close to or identical with *Machaeroprosopus*, and *Thecodontosaurus* teeth are at hand in our collections from the lowermost Chinle at St. Johns, Arizona.

Fossil Occurrences in the Chinle

We have explored most of the exposures in the Chinle but have not yet visited the small areas in northwestern Arizona nor those along the borders of Glen and Cataract canyons in southern Utah. Vertebrate fossils may be found throughout the exposures with the exception of those in Nevada and the region of St. George in southwestern Utah, which however contain fossil logs similar to those in the fossil forests of Arizona.

Almost everywhere the fossil bones occur in fragments, roughly broken or rotted prior to fossilization and sometimes slightly water worn. But at a few points, notably in the vicinity of Adamana, at St. Johns, and near Round Rock and Lukachukai in northeastern Arizona, extensive bone beds containing much good material have been discovered.

At all localities where identifiable fossils have been taken, with the exception of the fish localities at Zion Canyon and Kanab, the bones of phytosaurs constitute the greater part of the identifiable remains. Nearly everywhere these are associated with large amphibians, lung fishes, and the shells of the mollusc *Unio*, indicating fresh-water animal habitats of considerable uniformity throughout the region, and possibly similar climatic conditions over a wide area.

These fossil occurrences in the Lower Chinle together with what is known of the lithology and sedimentary history of this formation would most certainly indicate fluvatile conditions, presumably a great, low-lying flood plain near the

seacoast, traversed by slow-moving streams subject to occasional overflow and freshets, and interspersed with large swampy areas and shallow lakes with scattered stands of conifers on higher ground.

The headwaters of these streams apparently lay in a region of uplifted, marine limestones and shales of Permian age, subjected to repeated outbursts of volcanic activity with periodic deposition of rhyolitic ash. This seems to have been deposited by stream action, in lakes and across the face of the flood plains below. The mineral content of this ash may have varied somewhat at different periods of eruption giving the re-deposited bentonitic clays and arkoses the banded colors—white, gray, brown, yellow, blue, violet, red, purple, and black—that give these beds their striking coloration. During periods of volcanic quiescence, sand and gravel carried by the streams were deposited in lenses interstratified with beds of ash in the delta deposits. It is in the vicinity of these sandstone lenses, though in the clays themselves, that fossil bone deposits have usually been found, and there is a strange absence of good material elsewhere, even where fragments of bone are numerous.

It might be assumed that the banded colors in the variegated bentonitic clays are due to seasonal or periodic climatic change rather than to periods of volcanic activity. Answer might be given that beds of uniform color range in thickness from a few inches to ninety feet; that beds of such great thickness would require more time for deposition than that afforded in any one season; also that beds of bentonite of different colors are often separated by sandstone lenses, indicating a time interval during which sandy sediments were interposed between beds of transported volcanic materials. The changes in color between beds are often of such striking sharpness that they would scarcely be thought of as representing a gradual secular change.

The occurrence, in the same area, of thin fossiliferous beds alternating with considerable thicknesses of barren deposits invites especial attention to the conditions surrounding deposition and preservation of the remains. It is customary to find silicified wood in the gravelly and sandy layers where bones seldom occur; and bone material is most abundant in gray and blue layers of bentonitic clay within 400 feet of the base of the Chinle in the southeastern portion of the area of exposures. All fossil remains are less abundant in the upper limestone bedded zone of the Chinle (divisions A and B of Gregory) than in the lower zone (C and D of Gregory).

The harder portions of skeletons, dermal plates of amphibians, teeth, vertebræ, scutes and rostra of phytosaurs, and teeth and vertebræ of lung fish, far outnumber all other fossilized parts. Also, it is not uncommon to find skull elements of amphibians and phytosaurs dissociated along suture lines and scattered over small areas. Many bones, in the softer parts of the skeletons, show evidences of etching and decay before fossilization. In three localities a number of amphibian dermal plates and skulls have been recovered from an area of a few hundred square feet where scarcely any other parts of skeletons were found. What explanations may be given for such occurrences?

Among selecting and segregating agencies which may have been at work during the period between deposition and fossilization, the action of flowing water is perhaps the easiest factor to detect. Water-worn bone fragments are not uncommon, especially in the sandy layers, but in the vast majority of cases abrasive wear is not evident, even on small bone fragments. It is not believed therefore that stream segregation of material was a factor of great importance.

There seems to be evidence of trampling, mixing, breaking, and biting of bones by other animals, but it is unlikely, where quantities of bones are present, that all the lighter parts of numerous skeletons would be entirely disposed of by carnivores. Weathering before covering or before petrifaction was doubtless of frequent occurrence and would be selective in its action. But in many instances it seems that skulls and skeletons sank rapidly in oozy ground which later became subjected to great pressure from superimposed sediments resulting in flattening and crushing of the bones. In such cases there would be no weathering.

A factor that might be invoked to explain the absence of softer bones, the frequent occurrence of non-water-worn fragments, and the dissociation of skull elements would be the presence of a chemical agency in the water or mud. This might be, for example, a humic acid in swampy ground or a reagent derived from fresh rhyolitic ash carried by the streams. The effect of an acid reagent of this sort would be to etch out or destroy the softer parts of the skeleton leaving the harder, denser portions in great numbers just as they occur.

Occurrences of fossil wood and bone in the Chinle are so distributed that they might be taken to indicate periods of cataclysmic extinction. From the presence of great volcanic ash deposits and the frequent occurrence of pure charcoal lumps and charcoal encrusted logs in these deposits, it would seem at first thought that the bone beds and fossil forests may have been due to sudden destruction of life by volcanic outbursts, accompanied by fire and flood.

Objections to such theories are: the absence of completely preserved skeletons; the presence of bones apparently mutilated by other animals; the absence of fossil limbs and twigs; the scarcity of fossil bones in the horizons containing fossil logs, and the evidences of stream bedding at nearly every point where fossils are numerous.

Evidences of stream action are: interstratified and often cross-bedded sandstone lenses; fossil mud cracks and stream channels; water-worn pebbles and sand grains in the bentonite; transportation of charcoal fragments to some distance from logs, and lensing of bentonitic materials—more noticeable in respect to color differences than in actual composition of the various bentonitic layers.

It might be conceived that non-simultaneous occurrence of wood and bone deposits might be due to differential flotation and stream sorting of heavy and light materials. But in answer it should be urged that many logs are encrusted with charcoal in such a way as to indicate preservation where they were burned, the limbs and twigs being completely consumed and the logs charred. Also, it is rare to find skeletons which could have been transported as floating carcasses.

Most of the bone in the bone deposits is evidently from animals which have died in the immediate vicinity, bones of many sizes being found together, with little evidence of sorting. Coprolites are numerous in most localities where bones occur.

The possibility is evident that phytosaurs and amphibians did not live in timbered areas but confined their activities to the rush swamps and lakes, and this may in some degree account for the separation of wood and bone in the beds. However, it is apparent that the riparian association occupied by the animals is one that should traverse forested sections as well as more open country and should therefore have its representation of fossil wood as well as fossil bone.

Absence of extensive fossil bone deposits within the larger fossil log beds is probably fortuitous and due to relative paucity of extensive bone deposits anywhere in the Chinle with the chances against occurrence of large quantities of logs and bones in exactly the same horizons. The original forests were doubtless not continuous but occurred as patches of woods in occasional localities favorable to tree growth.

Exposures in the Lower Chinle are usually of the "badland" type—low rounded hillocks, sandstone-capped mesas, buttes and pinnacles surmounting intricately dissected slopes, and narrow, tortuous stream channels. The method of erosion is singular owing to the nature of the bentonitic clays constituting a large part of the deposits. The surface of these hard, blocky clays, when wet, absorbs moisture rapidly, swells, and breaks down into a sticky mud. This mud is almost impervious and forms a coating a few inches thick over the dry unaltered shales beneath. During heavy rainfall, the mud on steeper slopes collects in pellets which roll down into the stream channels, where they disintegrate and are carried rapidly away as suspended material.

In many places the bentonitic beds are traversed by numbers of small cracks along joint planes running at all angles through the mass. Percolating water during storm periods finds its way downward through these cracks and, if there is drainage to a lower slope, eventually comes to the surface again. Certain crevices may in this way become rapidly enlarged resulting in surface funnels leading downward from the hillsides into open shafts and tunnels sometimes a hundred feet or more in length. These funnel-cave systems are responsible for occasional destruction of specimens.

Swelling and pulverizing of the surface of the exposures lead to fracture and disintegration of much of the fossil bone material uncovered. Thus it is that much of the surface material is worthless and it becomes necessary to excavate beneath the pulverized surface layer for perfect specimens. Prospecting for specimens in the Chinle badlands involves careful search for fragments which have broken and rolled away from dry, unaltered material hidden in the shales.

The fossil wood in these beds occurs, for the most part, as agate and topaz. The fossil bone is usually made up of softer material. Preservation is good although there is a tendency in sandy layers to acquire a hard coating of limonite or hematite, which is in some cases difficult to remove without destroying the surface of

the specimen. Gypsum is found all through the beds, as a secondary deposit filling seams and joint cracks. Fossil bones becoming coated with this material are often partly or wholly rotted by it.

The finding of anything approaching a complete skeleton is a very rare occurrence. Complete skulls are more numerous, and dissociated skull elements, teeth, limb bones, and dermal plates, are often abundant.

I have not yet seen identifiable material from the lowermost "Shinarump" gravels. Bone fragments are abundant but are invariably broken and worn into small pieces.

Future studies upon the history of sedimentation during Chinle time will naturally be greatly aided by careful identification of the animal and plant remains. The fossil logs, which often show the cell structure beautifully in thin sections, will doubtless be found to include forms other than the two already described by Knowlton (1888), and Jeffry (1910). Perhaps differences in the flora at various levels of the Chinle might be discovered although it may be that differences in the manner of petrifaction account for much of the difference in the appearance of the wood in the various fossil forests.

Phytosaur Discoveries in the Chinle

Occurrence of phytosaurs in beds now recognized as belonging to the Chinle was first indicated by a mandibular fragment found in southeastern Utah by H. S. Gane and transmitted to the United States National Museum by Whitman Cross. F. A. Lucas (1898) described this specimen as a crocodile under the name *Heterodontosuchus ganei*. The type locality as reported by Cross is "Clay Hill divide, 20 miles east of the north end of Glen Canyon" of the Colorado River. From a distant and superficial inspection I should judge these beds to be at the base of what I call the Upper Chinle (bed B, of Gregory). The specimen is said to have only two of the anterior teeth enlarged, which would separate it from other known phytosaurs. Mook (1925) following Hay (1902) still includes this form with the crocodiles but gives no evidence beyond that in the original description. According to McGregor (1906), this species is also represented by other material, including a perfect axis, in the collections of the National Museum. It seems more probable, however, that these additional specimens are part of the Barnum Brown collection from Arizona and represent other forms of phytosaurs, probably the genus *Machaeroprosopus*.

Fossil vertebrates in the Chinle of Arizona were discovered by L. F. Ward (1901) in 1899 in a locality near Tanner Crossing on the Little Colorado River and near the First Forest in the Petrified Forests near Adamana. The following year Barnum Brown in the interest of the United States National Museum collected more material near Tanner Crossing. Ward's collection was examined by E. Fraas, and the collections made by Ward (1905) and by Brown were studied by F. A. Lucas (1901 and 1904) who determined the age as Triassic with "the same

combination of belodont and labyrinthodont as in the Keuper," Upper Triassic of Europe.

The material described as new was a species of stereospondylous amphibian, *Metoposaurus fraasi*—type, an interclavicle from five miles east of Tanner Crossing; and a new genus and species of reptile, *Placerias hesternus*, referred to the Cotylosauria—type, a humerus from three miles north of Tanner Crossing. Huene (1911*a*) confirms Lucas' reference of *Placerias* to the Cotylosaurs.

Case (1920*b*) identifies an interclavicle of *Metoposaurus* in the National Museum collections, from near Tucker Springs on the road from Winslow to Leupp, Arizona. The locality has been considered as Chinle (Gregory, 1917, p. 47) and as Moenkopi (Darton, 1925, p. 117; doubtless from a reading of Gregory [1917, p. 35]). No vertebrate remains, except tracks, are known from the Moenkopi. The only other formation in the vicinity of this find is the Shinarump or basal conglomerate of the Chinle. The specimen may have come from that formation.

Huene (1926) has reexamined and figured some of the National Museum material. He places most of it in the Middle Triassic and recognizes the forms *Episcoposaurus horridus* Cope, *Typothorax coccinarum* Cope, and some small undetermined saurischian vertebræ, all from Tanner Crossing. These he regards as "of uncertain level but thought to be Upper Triassic." He determines the Adamana collection as: "Parasuchian teeth and bones, among them being *Palaeoctonus orthodon* Cope and *P. dumblianus* Cope" of Middle Triassic age. This determination of both Upper and Middle Triassic forms at Tanner Crossing appears to be very improbable. The Adamana "*Palaeoctonus*" is doubtless based upon an anterior tooth or teeth of *Machaeroprosopus*.

In 1912 S. W. Williston and Paul Miller visited the Moenkopi beds at Holbrook, Arizona, and eastward into New Mexico in search of Permian vertebrates. Some material was obtained at this time from the Chinle Triassic in that vicinity.

In 1914 M. G. Mehl, then of the University of Wisconsin, made collections in the vicinity of Tanner Crossing and in the Chinle beds at Fort Wingate, New Mexico. This collection, together with one or two of Williston's specimens, previously collected, formed the basis of Mehl's reports (1915 and 1916) in the latter of which the phytosaurian genus *Machaeroprosopus* is described. The type skull was collected "two miles east of Tanner Crossing and perhaps two hundred feet above the Lithodendron member of the Shinarump" of Ward (1905). This horizon is in the Lower Chinle (division C of Gregory, 1917).

In the winter of 1905–6, John Muir gathered a small collection of vertebrate fossils in the Petrified Forests near Adamana which he presented to the University of California. Professor J. C. Merriam recognized in it some Phytosaurian remains and these have been studied in connection with the present report.

From 1909 to 1913, during a reconnoissance of the Navajo country, Herbert E. Gregory (1916, 1917) collected fragmentary vertebrate remains at various localities in the Chinle. These specimens are now in the Peabody Museum at Yale University. Some of these have been reported upon by Professor R. S. Lull as "not identified but with Triassic affinities."

In 1919 or thereabouts, Robert R. Alton secured a portion of a phytosaur lower jaw in a gravel lens just west of and immediately below the First Forest beds near Adamana, Arizona. This specimen is in the geological collections of Western Reserve University, Cleveland, Ohio. It has been sent to me for study through the courtesy of Dr. J. E. Hyde.

In 1919, Mrs. Ynez Mexia, during a visit to the Blue Forest, near Adamana, gathered specimens of fossil vertebrates which she presented to the University. Her discovery led to a reconnoissance of the region by Miss Annie M. Alexander and Miss Louise Kellogg in 1921. They collected excellent material in the Blue Forest beds and found a new locality in the Carrizo (Lithodendron) Wash, seven miles northwest of Adamana. These deposits were worked in 1921, 1923, 1924, 1926, and 1927 by field parties from this University.

The bone beds at St. Johns, Arizona, were discovered by Eustace L. Furlong in 1921, in the course of a geological reconnoissance of that region. This locality we worked in 1923, 1924, 1926, and 1927.

In the summer of 1926 a field party of the United States Geological Survey, working in eastern Utah under A. A. Baker, found fossil vertebrates in the Chinle. The locality is one and one-half miles due south of the town of Moab, and the horizon lies 133 feet below the base of the Wingate sandstone, but Dr. Baker points out that "there appears to be an angular discordance between the Wingate and Chinle at Moab so that the relation of the fossil-bearing beds to the Wingate sandstone at Moab may not be the same as that in a normal section."

The fossils were submitted to C. W. Gilmore for identification and his unpublished report reads:

> Proximal half of a right femur of a parasuchian reptile which may be identified (following Huene) as *Typothorax coccinarum* (Cope).
>
> A vertebrate centrum, some broken bone fragments and one tooth also pertain to parasuchian reptiles but none can be further identified.

The presence of *Typothorax* is taken to indicate Upper Triassic age of the beds.

These reports and sections of the Chinle made by members of Baker's party have been kindly furnished by Dr. George Otis Smith, Director of the United States Geological Survey.

In 1927, at the suggestion and through the courtesy of Dr. Baker, we visited the Moab fossil locality and made further collections there.

Occurrence of fossil vertebrates in beds near Kanab, Utah, which are probably to be regarded as Chinle Triassic, has been made known through the discoveries of C. D. Walcott (1880). Here, about 900 feet above the Shinarump conglomerate, is a ledge of brown sandstone containing ganoid fish scales and bones. We visited Kanab in 1923 and found what may be Walcott's original locality on the side of the bluff about a mile east of, and 400 feet above, the schoolhouse. The fossils occur in a lens of laminated sandstone a few inches thick. Fish scales and bones are very numerous in a small area. The occurrence and fauna are similar to those found in the Upper Chinle a few feet below the base of the Wingate cliff series, two miles south of Moab, Utah.

SAN RAFAEL SWELL
San Rafael River
GREEN RIVER
Green River
D & R G R R
Thompsons
Cisco
Grand River
Moab
Muddy River
Fruita
U T A H
CATARACT CANYON
Indian Creek
COLORADO
Henry Mts
Abajo Mts
Montecello
Verdure
Loc A277
Bears Ears
Blanding
Montezuma Creek
Clay Hills Divide
Comb Wash
SAN JUAN RIVER
Mexican Hat
Bluff
MONUMENT VALLEY
Navajo Mt
Navajo Mtn
Creek
Lee Ferry
Cliffs
Valley

Map A. Distribution of Chinle Triassic Formation as Exposed in Nevada, Arizona, Utah, and Western New Mexico. Areas in Northern New Mexico Not Shown. Museum of Paleontology Fossil Localities are Numbered.

Both at Kanab and at Moab the bones lie very thickly in a small area surrounded by exposures which are practically barren. It may be that these local accumulations are the result of the drying of small ponds that contained many fish.

There has been some speculation as to whether Walcott's beds at Kanab represent Triassic or Jurassic deposits. There is, however, no question as to the Triassic age of the similar deposit at Moab, and there is some reason to regard the two as contemporaneous.

In June, 1927, Mr. James P. Fox and I visited the exposures in the Upper and Lower Chinle near Lukachukai and Round Rock in northeastern Arizona. At both places some good material was obtained from bentonite beds 300–400 feet above the De Chelly sandstone at the base of the Chinle. We also collected in a number of localities in the Upper Chinle, including Kayenta, Arizona; and Bear's Ears, Indian Valley, Moab, and the canyon of the Grand River in Utah.

In October, 1928, Mr. V. L. Vander Hoof and I made collections of phytosaur skulls and other material from the vicinity of Canjilon in northern New Mexico. Data secured at that time lead us to correlate the upper four hundred feet of the Triassic shales, those lying immediately beneath the Wingate, with the Upper Chinle of Arizona and Utah.

Material and Localities

Our collections contain 105 lots of phytosaur remains from forty-six numbered localities in the Chinle Triassic of Arizona, New Mexico, and Utah (see map A). Of these lots, twenty-two are fragmentary and of value only as locality records; the remaining seventy-six numbered specimens include forty-nine skulls. Of these, seventeen are excellent study specimens, seven being complete or nearly so, and five of the seven are accompanied by associated lower jaws and other skeletal parts. One of the skeletons is complete except for the limbs and the greater part of the tail. All parts of the skeleton except portions of the feet and the hyoid bones are represented by this and other specimens.

All of the more nearly perfect phytosaur material in our collection has been taken in three general areas in Arizona: the vicinity of Adamana, the vicinity of St. Johns, and the exposures south and east of Round Rock in the Chinle Valley.

Phytosaur remains have been collected at the localities indicated on the accompanying maps. Map A illustrates the distribution of exposed Chinle sediments in Arizona, New Mexico, and Utah, together with the localities where fossil vertebrates have been found by our parties. Map B is a detail of a smaller area near Adamana, Arizona, showing the limits of certain localities mentioned in the systematic part of this paper.

All the localities in Arizona except 7048*c*, 7048, 7049, and 7049*c*; A273 near Round Rock and A275 near Kayenta are in the Lower Chinle (divisions C and D of Gregory). These localities as well as the localities in Utah and locality 7311 near Thoreau, New Mexico, are believed to be in the upper zone (divisions A and B of Gregory), equivalent to the Upper Chinle of this paper.

Stratigraphic Distribution of Species

One of the objects of our work has been to determine and to evaluate, if possible, the differences in phytosaur skulls from various horizons in the sediments of the Lower Chinle. This question involves several preliminary problems, the solution of which has had to await the accumulation of a sufficient number of specimens.

The recognition of specific forms in phytosaurs has always been a matter of doubt owing to lack of material adequate for the determination of individual, age, and sex characters. My estimation of the magnitude of these latter differences has been made through examination of numbers of skulls from single localities and stratigraphic horizons. Localities in the Petrified Forest region in eastern Arizona have furnished the critical specimens. The results, as subsequently outlined, show, I believe, that individual variation is not so great as to prevent the establishment of "species" on relatively slight but constant differences; that age variation, though pronounced, can be recognized and may be eliminated through the use of adult remains; and that proper allowance may also be made for sexual dimorphism in skull structure.

It is needless to say that for the purposes of this problem it becomes desirable to recognize as many "species" as can be established upon differences which are constant in any given horizon, or series of horizons, and at any given locality. I have accordingly proposed five new "species" from the Lower Chinle. Each of these occupies its own level or series of levels as determined by geologic studies. Whether these so-called "species" are to be regarded as mutants, varieties, subspecies, or "full species," is a matter of individual choice. I call them species because of the difficulty at present of discovering annectant or intergrading forms and because of the fact that certain of the characters are segregated stratigraphically. The fossils usually occur in narrow zones, separated by tens or hundreds of feet from superimposed or underlying fossiliferous beds. The differences between some of these forms are admittedly slight, and where exact determinations of stratigraphic level are not determinable it might be considered impracticable to draw such fine distinctions. I am convinced, however, that further stratigraphic correlations will become available with close study of the fauna of a series of levels such as are present in the Chinle.

My method has been to combine accurate field measurements of stratigraphic levels with systematic and phylogenetic studies. Field measurements of the relative levels of fossil horizons are not often obtainable in terrestrial beds owing to lensing and interbedding of the sediments, and the sparse distribution and areal separation of fossil localities. With a view toward the possibility of making such measurements, we have confined much of our collecting to a small area in the vicinity of Adamana, Arizona, where the phytosaur species *M. adamanensis, lithodendrorum,* and *tenuis* occur. Here it has fortunately been found possible, owing to the continuity of the exposures and the presence of extensive horizontal

members, to follow continuously a number of fossil horizons and to measure, with compass and spirit level, the differences in elevation between them.

In going over the ground, I have had the valuable assistance of Mr. James P. Fox. We have repeatedly walked over these beds, measured sections, and traced the more extensive lenses, with results as indicated on the accompanying chart (fig. 1).

The fossiliferous area at Adamana (see map B) is an elliptical one running more or less along the strike of the beds, northwest and southeast, with a length of about fifteen miles. The Carrizo exposures occupy the northwestern extremity of this area, the Blue Forest beds the center, and the Billings Gap the southeastern portion. The most extensive member in the stratigraphic series is a thick bed of gray-blue bentonite which underlies the whole district and extends several miles westward along the Puerco Wash. The Blue Forest fossil horizons containing *Machaeroprosopus adamanensis* lie within this member. Above it the beds become more sandy, contain thin purple and violet bands, and they are capped by another extensive series consisting of thick lenses of sandstones and conglomerates. The hardest and most conspicuous of these sandstone layers forms the tops of the buttes one mile south of the Blue Forest, as well as the top of the mesa above the First Forest and the lowermost terrace at the Point of Bluff and on the Twin Buttes. From here it may be traced across the top of the small butte southwest of Carrizo Station, and it appears again on the south bank of the Puerco opposite the junction with the Carrizo Wash. On the north side of this Wash it outcrops in a low rocky bluff and from here it may be followed into the mouth of Digger Creek and the mouth of the Carrizo about a mile north of the road bridge. In the Carrizo it becomes an extensive bed of hard brown sandstone upraised in a gentle anticline the apex of which lies in the badlands about four miles northeast of the road bridge. In this vicinity fossils occur above and below it in considerable quantity. The type locality of *M. lithodendrorum*, from which all but one of the skulls of this species were collected, was a small area twenty feet below this brown sandstone in the apex of the anticline.

Starting again at the Blue Forest, the capping beds may be followed south for three miles to Billing's Gap where they lense out and pass into a thin layer of limestone bone breccia. It is just above this layer that the type skull of *M. tenuis* was found. A continuous series of exposures westward from this locality for a mile or more enables us to establish the level of the second skull of *M. tenuis* as almost exactly that of the type.

Returning to the Blue Forest, we find that the thin northern edge of the sandstone lens, which caps the Pictograph Bluff, lies forty feet below the lower fossil horizon of the Blue Forest beds (type locality of *M. adamanensis*). This so-called Pictograph Sandstone dips slightly to the northeast and may be followed without interruption four miles northward to the Puerco Wash, where it lies about forty feet above the Wash and about sixty feet above the station at Adamana. At the latter point there is a deep artesian well-boring, the log of which has been recorded

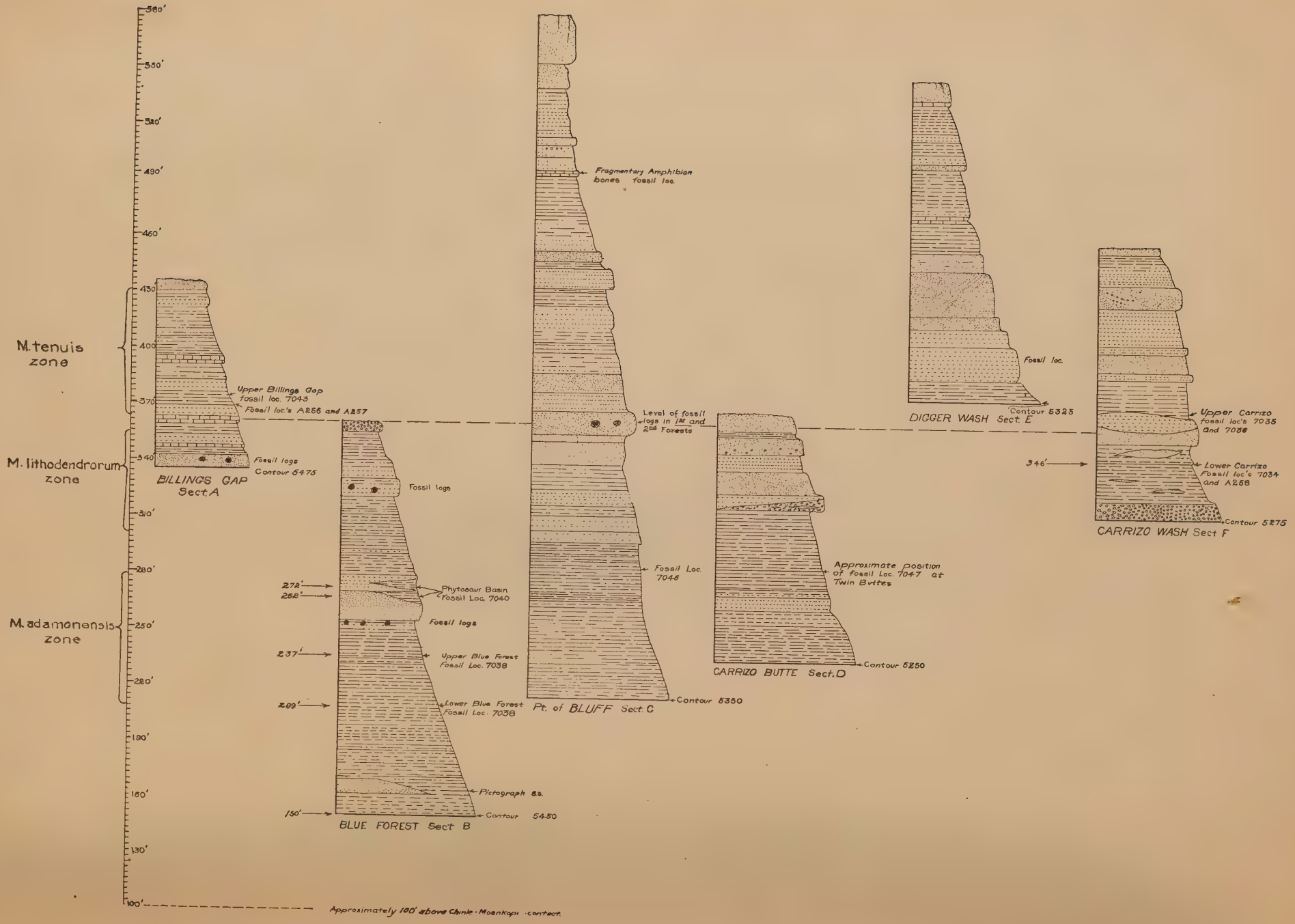

M. tenuis zone
M. lithodendrorum zone
M. adamanensis zone
BILLINGS GAP Sect. A
Upper Billings Gap fossil loc. 7043
Fossil loc's A256 and A257
Fossil logs
Contour 5475
BLUE FOREST Sect B
Fossil logs
Phytosaur Basin Fossil Loc. 7040
Fossil logs
Upper Blue Forest Fossil Loc. 7038
Lower Blue Forest Fossil Loc. 7038
Pictographs
Contour 5450
Pt. of BLUFF Sect. C
Fragmentary Amphibian bones fossil loc.
Level of fossil logs in 1st and 2nd Forests
Fossil Loc. 7046
Contour 5350
CARRIZO BUTTE Sect. D
Approximate position of fossil Loc. 7047 at Twin Buttes
Contour 5250
DIGGER WASH Sect E
Fossil loc.
Contour 5325
CARRIZO WASH Sect F
Upper Carrizo fossil loc's 7035 and 7036
Lower Carrizo Fossil loc's 7034 and A258
Contour 5275
Approximately 100' above Chinle-Moenkopi contact

Fig. 1. Stratigraphic sections taken at various points in the Lower Chinle near Adamana, Arizona (cf. map B). Columns indicate total available height of exposure at each station. Broken lines of correlation between sections indicate approximate positions of fossil localities.

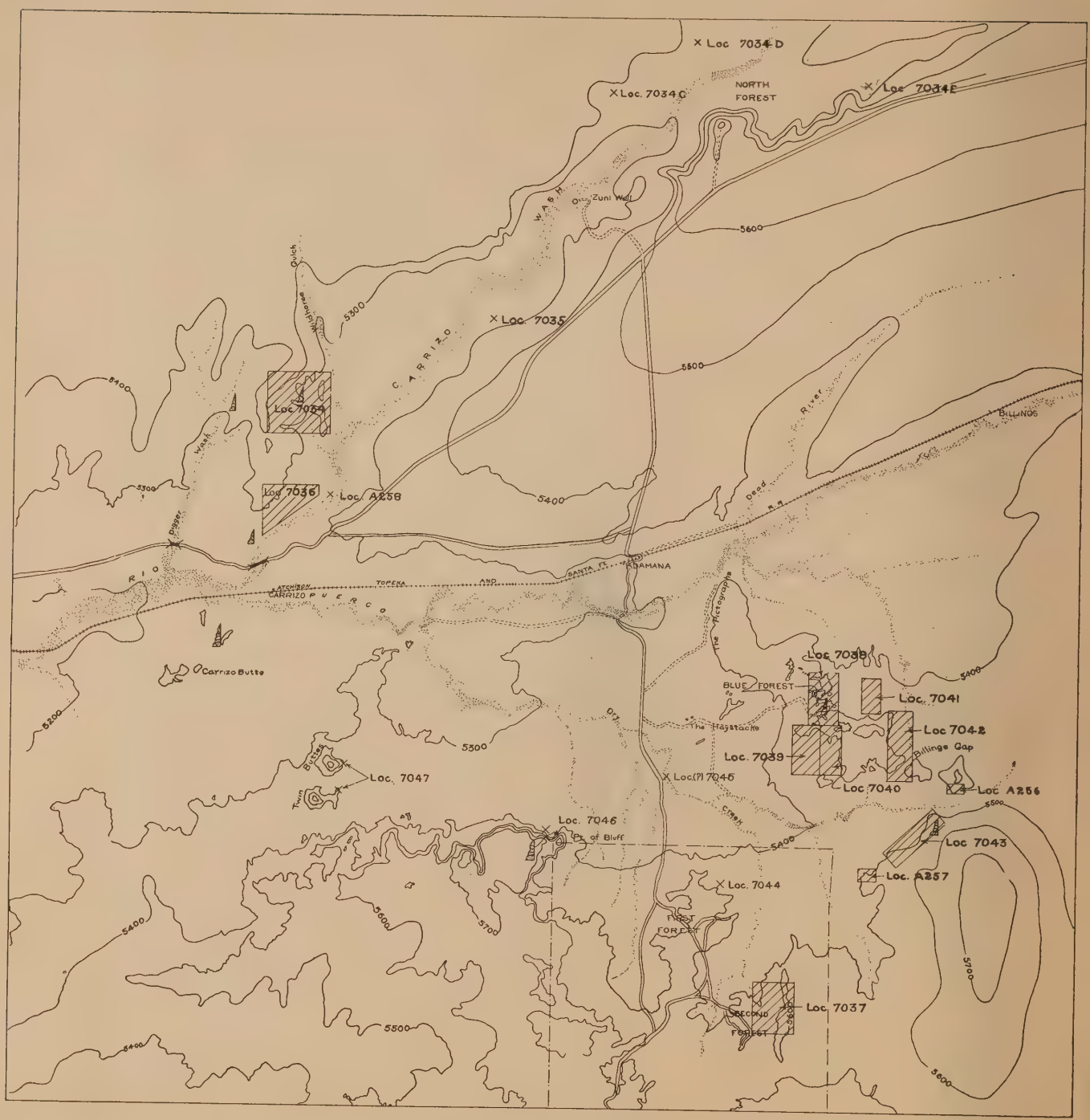
by Ward (1901). This log shows that Adamana Station lies one hundred feet above the top of the Moenkopi beds (in which salt water occurs). All this gives us the elevation above the base of the Chinle-Shinarump of all the fossil horizons in the Adamana district. As shown on the accompanying chart these lie from 209 to 490 feet above the base of the Chinle.

Between the Adamana district and the fossil localities at St. Johns, a distance of over forty miles, there are several gaps in the exposures which do not permit of direct tracing of the various levels. The lower fossil beds at St. Johns however lie only from 15–50 feet above a well marked local unconformity, which apparently marks the base of the Chinle-Shinarump. Below this unconformity are beds of hard, red, ripple-marked sandstone which I take to be the Moenkopi.

It seems certain that the type locality of *M. zunii* lies close to the base of the Chinle in the St. Johns district. Lithologically the beds near the base of the Chinle at St. Johns and at Adamana are similar. Those at Black Mountain about halfway between the two points show a five-hundred-foot section of the Lower Chinle which includes thick, gray-blue, bentonite layers two hundred feet above the top of the Moenkopi just as at Adamana. I therefore feel safe in assuming that the base of the Chinle at St. Johns represents about the same depositional period as the base of the Chinle at Adamana. If this be so, the lower St. Johns fossil horizons are at least one hundred and fifty feet below the lowest fossil horizon at Adamana.

We must now consider the occurrences at Round Rock and Lukachukai in northeastern Arizona, where there are again thick beds of bentonite, unmistakably in the Lower Chinle and containing several fossil horizons. The exposures here are very high and permit accurate measurements down from the base of the red sandstones, shales, and mottled limestones of the Carson Mesa series which constitute the base of the Upper Chinle (divisions A and B of Gregory, 1917). According to Gregory's sections (p. 43) the type horizon of *M. gregorii* lies somewhere within his bed No. 22, 420 feet in thickness. He describes this as made up of "Shales and Marls [bentonite], highly colored red, purple, grey, ... petrified wood in chunks and trees abundant, especially near the top; all beds calcareous and friable; forms badland topography." This is in Gregory's division C of the Chinle.

Fox's section (MS) at the type locality of *M. gregorii*, three miles southeast of Round Rock would indicate that this horizon is 325 feet below Gregory's No. 20, which according to Gregory's data would place it about 330 feet above the base of the Chinle. Other specimens of *gregorii* have been obtained at the base of the badland exposures six miles west of Lukachukai, Arizona. These exposures lie about 10 miles east of the type locality. One hundred and seventy feet above the *gregorii* horizon just south of Round Rock is another meager fossil bed in limestone conglomerate from which was obtained a phytosaurian squamosal similar in form to those of *M. tenuis* of the Adamana region.



Map B. Collecting localities in vicinity of Adamana, Arizona. Small stratigraphic columns indicate points at which sections in figure 1 were taken.

There now remains a question as to the stratigraphic position of the two species of *Machaeroprosopus* which have been described by Mehl (1916 and 1922). The first of these is *M. validus* from Ward's fossil locality near old Tanner Crossing in the valley of the Little Colorado, Arizona. Mehl states that his type skull came from "perhaps two hundred feet above the Lithodendron member of the Shinarump group of the Triassic." Ward (1905, vol. 1, p. 39) in his section through this fossil locality indicates a thickness of 500 feet for his "Lithodendron member" which includes the Shinarump conglomerate at its base. This would place the type horizon of *validus* at about 700 feet above the top of the Moenkopi (base of the Chinle-Shinarump).

It seems likely that Ward's estimate of the thickness of the "Lithodendron" is too great, and that the level of the bone bed is less than 700 feet above the base of the formation. Apparently however the horizon of *validus* is at least 200 feet above the level of any of the phytosaur horizons from which we have described new forms. It is significant that *validus* is markedly different from any of our species.

The second of Mehl's species is *M. andersoni*, described (1922) from an unrecorded locality in the "Triassic of Guadaloupe County, near Santa Rosa, New Mexico." Certain of the characters of this skull indicate relationship to my species *M. tenuis*. It is unfortunately impossible to say anything at this time concerning the stratigraphic level of the find. It may occur in the upper part of the Dockum.[2]

I now submit in tabular form (table 2) certain differences between the various skulls of *Machaeroprosopus* so far discovered in the Lower Chinle beds. It may be said that only three of the characters tabulated show a tendency toward what might be called "orthogenetic" or progressive change. Of these three the most interesting is the narrowing and depression of the supratemporal fenestra and its almost complete obliteration in *validus*. This is illustrated in the accompanying figure (fig. 2), which may be compared with those of Mehl *et al.* (1916).

The change in the position of the anterior boundary of the parietals seems to accompany and perhaps to be a result of the depression of the fenestræ. It appears that the parietals encroach more and more upon the frontals as the posterior boundaries of the fenestræ move downward and forward. In the primitive phytosaurs *Paleorhinus*, *Mesorhinus*, and others, as well as in many related reptiles, the supratemporal fenestra develops its posterior boundary at a level with the skull roof. The depression and finally the folding of the posterior boundary in under the skull roof are correlated with a great elevation of the quadratojugal region and the further mechanical advantage of bringing the occipital condyle as far forward and as far downward as possible. This is all apparently a method of overcoming the difficulty of supporting, from the neck vertebræ, a massive skull of from three to four feet or more in length. There is some reason therefore

[2] A third species recently described by Mehl (1928*a*) from 7 miles NE of Adamana comes from an unrecorded horizon presumably above the level of *M. lithodendrorum*.

TABLE 2

COMPARISON OF SKULLS OF *Machaeroprosopus* IN LOWER CHINLE BEDS

Species and stratigraphic level above base of Chinle-Shinarump.	Teeth: Upper / Lower	Squamosal: Length / Height	Rostrum: ♂ Adult / ♀ Adult	Premaxillaries: Degree of enlargement of posterior alveoli.	Postorbital-squamosal bar: Width	Parietals: Position of anterior suture and shape of post-processes.	Parietals: Excavation of supratemporal fenestra.	Lower jaw: Length of squamosal / Length of jaw	Lower jaw: Length of splenial / Length of squamosal	Lower jaw: Number of alveoli opposite symphysis.
M. zunii 15–60 feet	?	1.08–1.17 / 1	Long and slender, no crest / ?	?	Narrow	Behind posterior margin of orbit	Broad and to depth of nearly half the length of the parietal.	Symphysis very long	?	?
M. adamanensis 209 + feet	40–43 / 44–45	1.15–1.28 / 1	Long and slender, short crest / Long and slender, short crest	Slight	Narrow	To or behind posterior margin of orbits.	Broad and to depth of nearly half the length of the parietal.	1 / 2.3	1 / 1.8	32–33
M. gregorii ±300 feet	41 / 47–48	1.06–1.08 / 1	Short and massive, moderate crest. / ?	Greatly enlarged in old adults.	Narrow	Behind posterior margin of orbit.	Broad and to depth of about third of length of parietal.	1 / 2.6	1 / 2.1	35
M. lithodendrorum 335–346 feet	44–45 / 47–49	1.43–1.74 / 1	Short and massive, elongated crest. / Probably the same.	Greatly enlarged in old adults.	Narrow	To or beyond margin of orbit.	Broad and to depth of third of parietal or less.	1 / 2.6	1 / 2.0	34
M. tenuis 375+ feet	42–45 / 49–50	1.75–2.07 / 1	? / Long and massive, no crest	Gradually and moderately enlarged in old adults.	Broad	To or beyond orbits	Narrow and to depth of only fourth of parietal.	1 / 2.2	1 / 1.9–2.2	34–35
M. andersoni ?	47–48	?	Long and heavy, no crest	Abruptly enlarged	Broad	Well beyond margin of orbit	Narrow and to depth of only fourth of parietal.	?	?	?
M. validus ±600 feet	37 / 39–40 / 3 anterior teeth enlarged	±1.45 / 1	? / Short and massive, short crest	Not enlarged	Broad	Well beyond orbits	Broader by elimination of parietal processes.	1 / 2.6	?	28

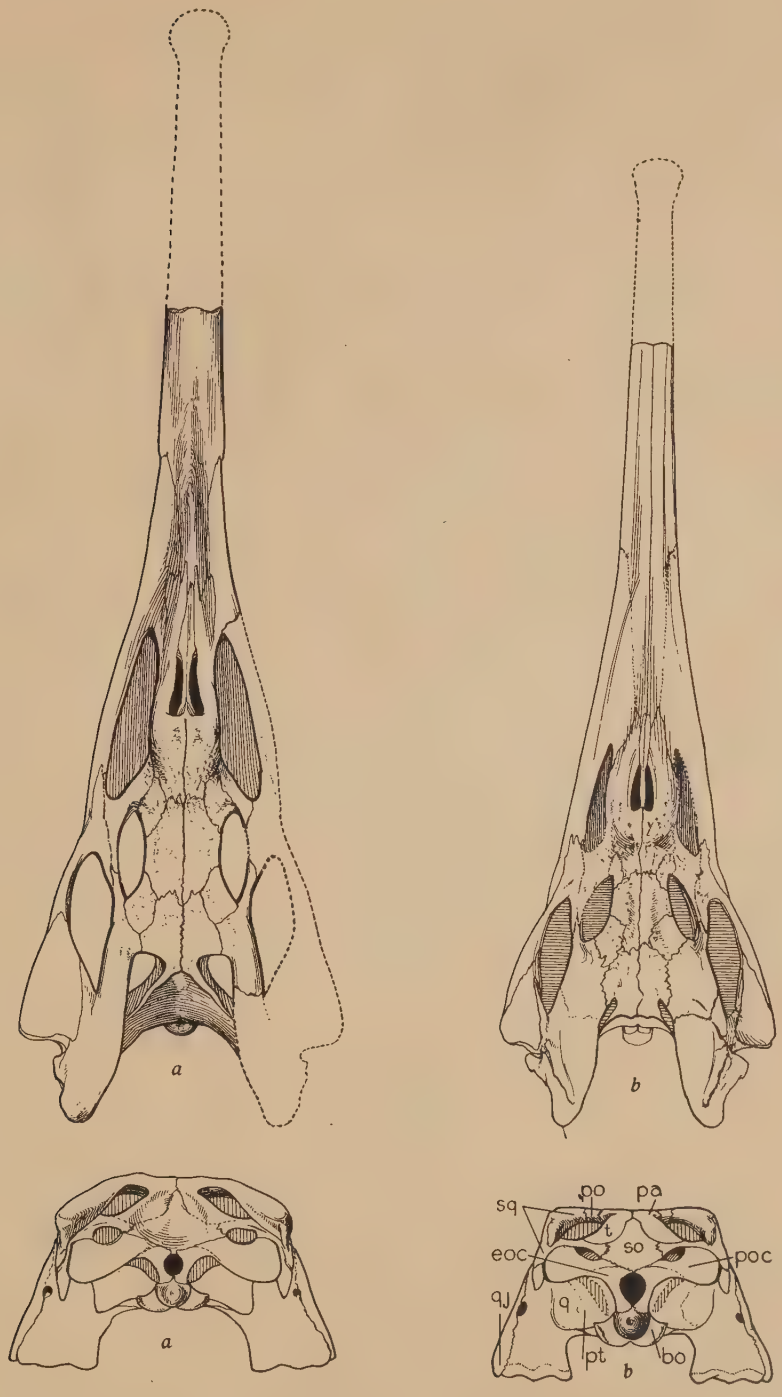


Fig. 2. *a. Machaeroprosopus lithodendrorum*, 7034/26719 and *b. M. tenuis* (type), 7043/27018, ×1/6.

to believe that the depression of the supratemporal fenestræ is an adaptive change that went on independently in various groups of phytosaurs. It probably should *not* be regarded as an indication that the present series of seven species represents an actual descent line.

The width of the postorbital bar also increases as the antero-dorsal margin of the supratemporal fenestra becomes narrower. The widening of this bar finally involves the dorsal rim of the squamosal in the species *tenuis* (and *validus?*). The dorsal rim turns inward to form a characteristic flat surface in these species; this surface being a continuation of the postorbital bar.

Other characters, it may be stated, appear to be in the nature of mutants which become fixed in certain species and change, from time to time, independently and without adjusting themselves to any progressive scheme.

The teeth appear to increase slightly in number and finally show a marked decrease. The squamosal, which is broad, flat, and short in *zunii*, becomes thickened in *gregorii*, and elongated, narrow, and thickened in *lithodendrorum* and *tenuis*. In *validus* it has something of the character of *lithodendrorum*. This element is quite constant within the different horizons and furnishes one of the best indices to specific determination when found among fragmentary remains. It plays an important rôle in the support of the unwieldy head through the attachment which it furnishes for powerful dorsal neck muscles. The insertions of these muscles upon the squamosal were evidently more tendinous and perhaps more powerful in the case of the thickened, roughened, and elongated squamosals than in the earlier forms having a broad, smooth squamosal process (fig. 3).

The shape of the rostrum, the development of its crests, and the general proportions and massiveness of the snout are so variable on account of individual and age differences

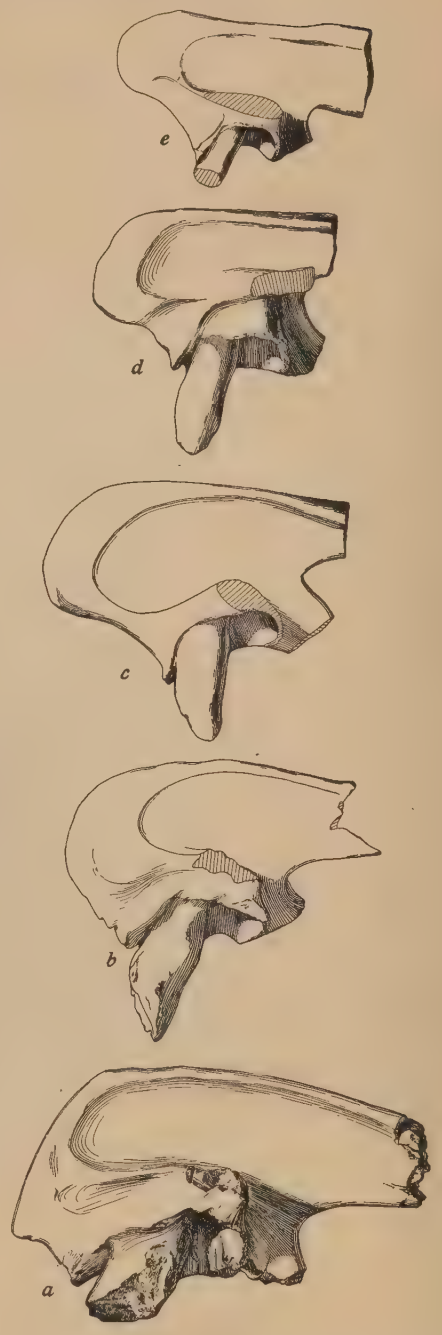


Fig. 3. Series of squamosal processes of *Machaeroprosopus* from a sequence of horizons in the Lower Chinle. *a. M. zunii*, 7307/27048, from 20 feet above Moenkopi-Chinle contact. *b. M. zunii*, 7307/27159, 60 feet above Moenkopi-Chinle contact. *c. M. adamanensis*, 7040/27007, 262-foot level. *d. M. lithodendrorum*, 7034/26719, 346-foot level. *e. M. tenuis* (type), 7043/27018, 375-foot level. All median side, ×1/3.

that it becomes difficult to estimate the phylogenetic significance of the characters involved. They may be correlated with changes in food or fighting habits. It may be said that massive, heavy-snouted forms have not yet been found in the lower levels (*adamanensis* and *zunii*) while they predominate in the middle levels among fully grown skulls. Correspondingly there is a tendency in some of the later species to greatly enlarge the posterior premaxillary teeth, but this character seems not to be expressed in *validus* (cf. fig. 11).

The length of the symphysis of the lower jaw is shorter in the forms with stout rostra, but the number of teeth opposite the symphysis seems to vary indiscriminately in the series. The length of the symphyseal portion of the splenial is also shorter in some of the more massive skulls.

A final question may be raised as to whether this series of forms represents a genetic sequence. The differences are mostly of small magnitude and the species should be admitted, I believe, into the category of a single genus. Certainly the species *zunii*, *adamanensis*, and *lithodendrorum* represent a closely related group of forms. They may even approximate a direct sequence of *recognizably distinct forms*, which means that intergrades between these forms would have characters so slight as to be negligible in a small series of specimens.

The form of the squamosal of *zunii* in the upper horizons of *zunii* is more similar to *adamanensis* than in the lower levels. A late form of *adamanensis* (65 feet above the type), approaches *lithodendrorum*. *M. gregorii* is close to *adamanensis* in some characters, to *lithodendrorum* in others. Its squamosal has much more the appearance of *adamanensis* than of *lithodendrorum*, but its measurements agree more closely with *lithodendrorum*. The squamosal of *gregorii*, has become thickened as in *lithodendrorum*.

I believe that the species *zunii*, *adamanensis*, *gregorii*, perhaps, and *lithodendrorum* give us what approaches an actual sequence of forms, as seen in the outline of the squamosal process (fig. 3).

The species *tenuis*, *andersoni*, and *validus*, on the other hand, I regard as distinct enough to question their place in the series. They may be regarded as invaders for the following reasons: *lithodendrorum* quickly disappears and is replaced by *tenuis* within a few feet of sediments, and this occurrence is also marked by the intrusion of another parasuchian genus, *Typothorax*. *Validus*, appearing later, is accompanied by still another faunal element, the genus *Placerias*, which does not occur in the lower horizons. *Validus* is sufficiently distinct to represent a second incursion of perhaps a more highly modified type of animal. More cannot be said of this until the other elements of the Chinle fauna are studied.

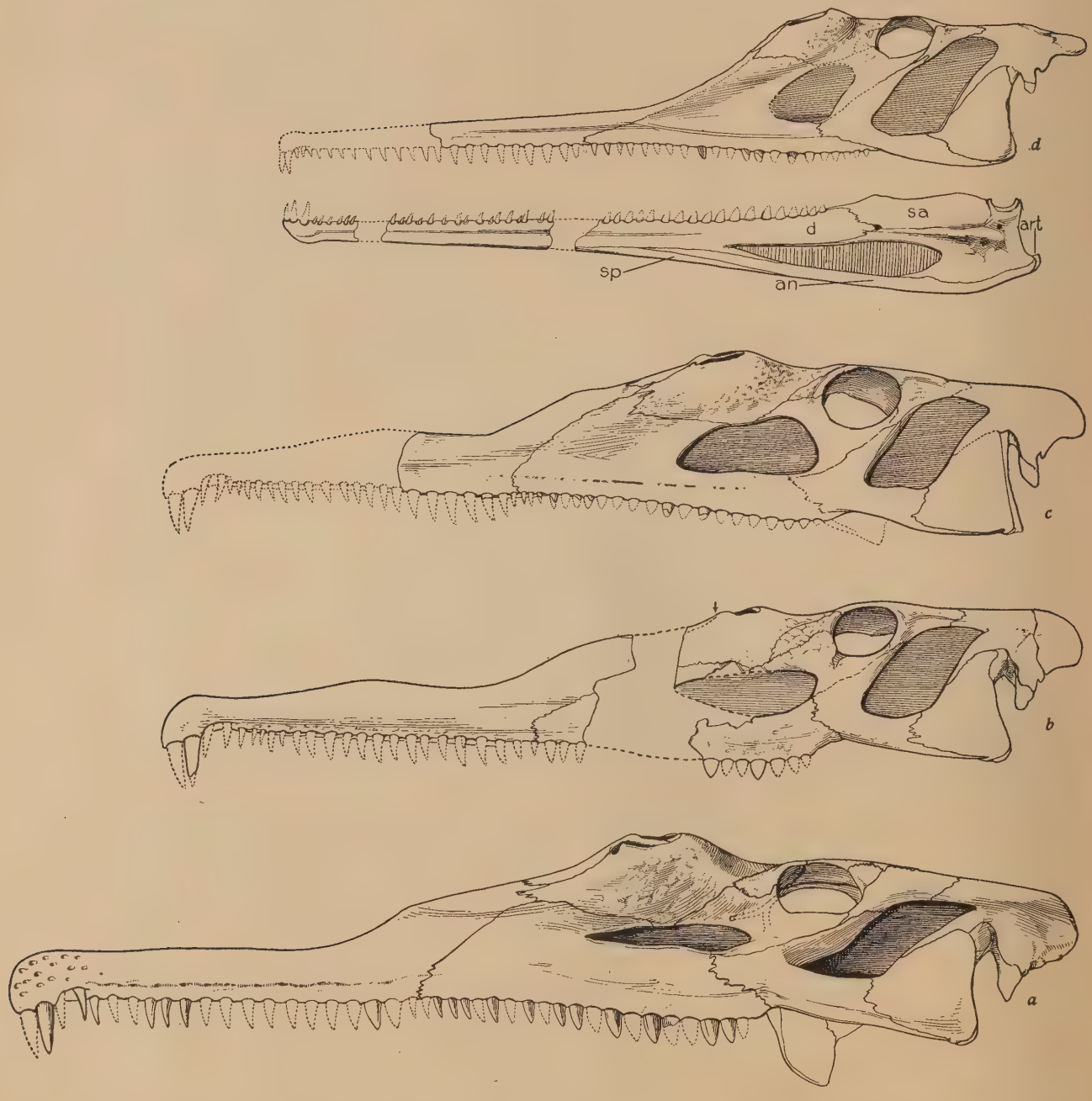


Fig. 4. Series of skulls of *Machaeroprosopus* from a sequence of horizons in the Lower Chinle. *a. M. adamanensis* (type), 7038/26699, 209 feet above Moenkopi-Chinle contact. *b. M. adamanensis*, 7040/27007, 262-foot level. *c. M. lithodendrorum*, 7034/26719, 346-foot level. *d. M. tenuis* (type), 7043/27018, 375-foot level. ×1/6.

SYSTEMATIC DESCRIPTIONS

Age and Sex Differences

Thirteen of our best phytosaur skulls have been secured in an area near Adamana, Arizona, where it has been possible to determine the relative stratigraphic level of each find. Five of these were found in exactly the same layer on the mud-cracked surface of what appears to be a delta deposit in the Carrizo, covering about twenty acres of present exposure.

These five skulls vary in length from 688 to 1215 mm. including the second smallest and the second largest phytosaurs so far obtained from the Chinle. The differences between these skulls are very striking. They involve appearance, contour of snout, proportions, number and spacing of teeth, and relative location

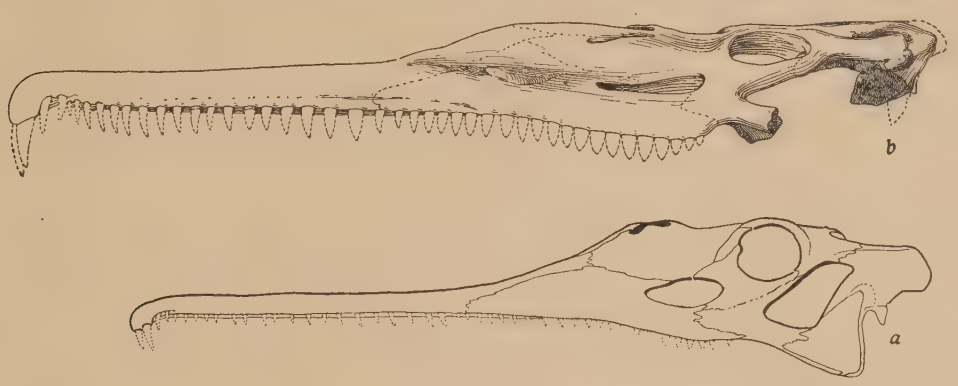


Fig. 5. Juvenile skulls of *M. lithodendrorum*, cf. figs. 4*c* and 11*c* for older skulls from same locality and horizon. *a*. 7034/27181. *b*. 7034/27179. ×1/6.

of internal and external nares. Had the small skulls been found in localities apart from the larger ones, it would have been hard to escape the conclusion that they should represent different forms. In fact, they differ in some characters which have been used to separate the main groups of phytosaurs. I am convinced, however, that they are of the same species since the characters all grade into one another in skulls of intermediate size (figs. 5, 11). Finally it may be observed that both large and small skulls from the lower Carrizo horizon—eight skulls and four additional squamosal tips—show constant characters (such as the form of the squamosal bone) that separate them from the species in the other horizons of the Adamana district.

It therefore appears that an extreme degree of age difference is to be found in these phytosaurs. The phytosaurs, of this group at least, have proportionally longer and more slender snouts in the young than in the adult. Very young skulls are not known but a fragment of a lower jaw (anterior portion of left dentary)

in our collection (27104) indicates a skull of only about 410 mm. in total length. The total length of this fragment (containing 23 alveoli) is 165 mm. and its depth at the level of the twenty-second alveolus is 17 mm. (a ratio of about 1 : 10). The length of a similar segment of a perfect adult jaw found in the same locality and horizon is 310 mm. and the depth at the twenty-second alveolus, 55 mm. (a ratio of about 1 : 6). This indicates a remarkable slenderness in the very young snout, which contrasts strangely with the conditions in crocodiles and alligators, where the young have proportionally shorter rostra than the adults.

The ratio of prenarial to postnarial length (measured from the anterior border of the nares) is an index of the relative elongation of the snout. Applying this measurement to nine skulls in our collection, we find that the ratio is considerably higher in the smaller skulls. This indicates that acceleration in snout growth in the young outstrips the rest of the skull, as shown in table 3.

TABLE 3

RATIOS OF PRENARIAL TO POSTNARIAL LENGTH

Locality and specimen	Total length	Prenarial / Postnarial	Ratio	Ratio of postnarial length to total length of skull
	mm. *inches*			
Blue Forest (*M. adamanensis*)				
26699 (nares elevated)	1095=44	618/477	1.36 : 1=4 : 3	42%
27007 (nares elevated)	951=38	570/381	1.50 : 1=3 : 2	40%
Billings Gap (*M. tenuis*)				
27018 (nares elevated)	819=33	513/306	1.68 : 1=5 : 3	37%
27149 (nares elevated)	1169=46	628/541	1.17 : 1=8 : 7	46%
Carrizo (*M. lithodendrorum*)				
26688 (nares depressed)	1215=48	660/555	1.19 : 1=6 : 5	46%
26719 (nares depressed)	965=38½	546/399	1.37 : 1=4 : 3	42%
27179 (nares elevated)	815=32	510/305	1.67 : 1=5 : 3	37%
27181 (nares depressed)	678=26½	419/259	1.62 : 1=5 : 3	38%
Round Rock (*M. gregorii*)				
27200 ♂ (nares depressed)	1230=48½	671/559	1.20 : 1=6 : 5	46%

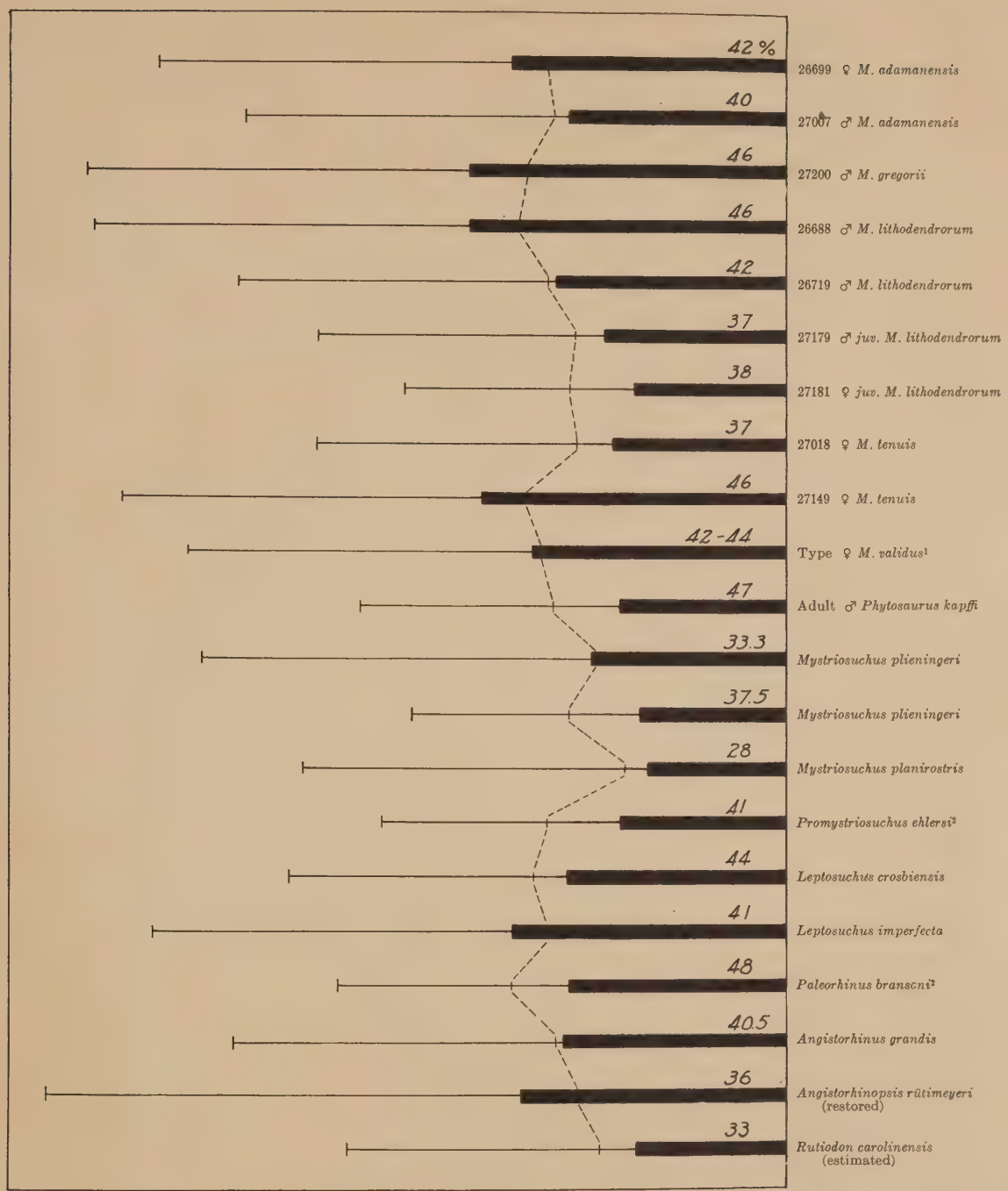


Fig. 6. Ratios of prenarial to narial-postnarial lengths in a number of known phytosaur skulls. Drawn to a scale of 1/10. Considering all skulls to be reduced to an absolute length of 10 cm., the narial-postnarial length of each would be indicated by the segments at the right of the dotted line.

Footnotes: 1. Measured on Mehl's drawings, which do not agree. 2. Anterior position of nares in *Promystriosuchus* and *Paleorhinus* makes rostrum appear unduly short.

It is obvious that the rostral ratio is an age character almost useless in comparing species of *Machaeroprosopus* unless comparable ages are selected. This is a matter of difficulty. The subjoined chart (fig. 6) includes data on the rostral ratio of all complete skulls known at the present time.

Variations in the contour of the rostrum and the development of dorsal crests are puzzling. It has been stated that, in some of the old-world forms, aberrant swellings and large pits, generally found on the dorsal surface of the snout, are due to diseased growths occurring in bite wounds which are inferred to be the results of combat (Abel, 1922; Moodie, 1922; Nopsca, 1926). It is also inferred that combats of this sort took place more frequently among the males and that the most highly crested forms are therefore males. The slender-snouted forms on this view are females and should not be regarded as distinct species. A high degree of sexual dimorphism should accordingly be expected in adult skulls. Let us see whether this is the case in *Machaeroprosopus*.

We have, from the lower 275 feet of the Chinle, eight adult skulls which show the contour of the rostrum. None of these have elongated crests. Two from the lowest horizons have no crests. Six from the 200–275-foot levels have crests reaching only to the posterior alveolar borders of the premaxillaries. From the next 85 feet of sediments there are seven adult skulls in our collections. All these have elongate rounded crests extending to the tips of the premaxillaries. Above the 360-foot level there are two adult skulls, one of which *M. validus* has a short crest and the other *M. tenuis* a heavy, rounded snout without crests.

One would infer from this that the development of the crest is a specific rather than a sexual character of adult skulls; that both males and females have it in some species and do not have it in others; and that there is no *pronounced* sexual dimorphism in *Machaeroprosopus*.

Any sexual differences appearing in these skulls should not be segregated into the various horizons but should appear in the specimens as a whole. Among sixteen skulls of *Machaeroprosopus* in which the character can be determined, there are ten in which the borders of the nares are at the level of the skull roof. Two of these are in the first 100 feet of strata, three in the next 175 feet, and five in the next 100 feet. The other six skulls have the borders of the nares elevated into a "crater" which projects above the level of the skull roof. One of these skulls is at the 209-foot level (type, *M. adamanensis*), another is at the 246-foot level, two more at the 275-foot level, and the character is shown in Mehl's types of *M. validus* and *andersoni* presumably from still other horizons. This character appears in young as well as in full-grown individuals, but seems difficult to recognize in adult crested forms owing to growth of crests up to the level of the nares. Consequently, I do not believe that in adults of the crested species it can be relied upon to distinguish the sexes. It is present in a young individual of the crested form *M. lithodendrorum*.

While the evidence is not conclusive, I regard the forms with "crater-like" nares as females. None of these attain the greatest size. In the type of *M. gregorii*,

which is the largest individual known among phytosaurs, the tips of the premaxillaries contain three large pathologic pockets which penetrate the bone, and the dorsal crest is slightly excavated by a number of small roughened pits. There are in fact more of these pits in this specimen than in all the others at hand, which would suggest, on Abel's hypothesis, that the individual was a male. The specimen has no raised borders around the nares.

One of the most variable skull characters of *Machaeroprosopus*, and of some other genera, is the dorsal swelling near the middle of the premaxillary part of the rostrum. This swelling is largest on a middle-sized individual of *M. adamanensis* (no. 27007), on a specimen of *M. lithodendrorum* of the same age (no. 26719), and on an adult of *M. tenuis* (no. 27149). It is very small on the adult type of *M. adamanensis* and on a specimen of *M. zunii* in which a portion of the rostrum is preserved. It is absent in all young skulls and has apparently been included in the posterior rostral crests in the heavily crested adults of *M. lithodendrorum* and *M. gregorii*. It is absent in *M. validus* and *M. andersoni*.

I should regard this variable character as a local expression of the general enlargement of the crest, in the species *lithodendrorum* and *gregorii*, and as an individual variant in *M. adamanensis* and *M. tenuis*. It appears to attain its maximum development in middle-sized individuals of *M. lithodendrorum*.

Another character relatively more pronounced in the larger skulls in our material is the lateral expansion at the posterior alveolar borders of the premaxillaries. This swelling accommodates four or five enlarged and elongated teeth on the middle of the upper jaw. It is not present in the type skull of *Machaeroprosopus validus* Mehl but is seen in *M. andersoni*, where it involves only three teeth. In *Machaeroprosopus* (*?*) *buceros* and in *Phytosaurus kapffi*, it is apparently but slightly developed. In *Palaeorhinus* and *Leptosuchus* it is carried forward nearly to the terminal expansion of the premaxillaries.

This posterior premaxillary enlargement is not present in our smallest skull (688 mm.). It is scarcely evident in skulls of 811 and 851 mm. It becomes very pronounced in skulls above 1000 mm. in total length, and reaches its largest relative proportions in the largest skulls. While it is differently developed in our species than in those previously described, its retardation during growth should be appreciated when considering specific differences.

From table 4 it is apparent that the antorbital fenestræ are relatively smaller in the smaller skulls than in the larger skulls. We are evidently dealing here with another age character. It is likely that the increase in size of this fenestra stands in direct ratio to the increase in size and massiveness of the lower jaw, this being doubtless due to great increase, during life, in the size of the anterior pterygoid muscles.

The longest diameter of the fenestra is compared with the length of the eye as a constant since it can be shown that the relative size of the eye decreases but little during growth.

Other characters apparently subject to change during growth are the shape, spacing, and differentiation of the teeth. In small skulls from all horizons, the teeth are more regularly and widely spaced, less highly differentiated, and the posterior teeth are more cylindrical at the base than in adults. In large specimens the alveolar septa become thinner owing to crowding of the teeth, the posterior premaxillary and maxillary teeth become relatively larger, and several of the smaller anterior premaxillary alveoli sometimes disappear (p. 46).

TABLE 4

SIZE OF ANTORBITAL FENESTRÆ

	Diameter of antorbital fenestra		Ratio of length of antorbital fenestra to diameter of eye
	Long	*Short*	
Blue Forest (*M. adamanensis*)			
26699 ♀	161	57	$\frac{161}{87} = 1.85$
Billings Gap (*M. tenuis*)			
27018 ♀	85±		$\frac{85}{62}\pm = 1.37$
27149 ♀	185	90	$\frac{185}{100} = 1.85$
Carrizo (*M. lithodendrorum*)			
26688 ♂	204		$\frac{204}{100} = 2.04$
26719 ♂	142	53	$\frac{142}{75} = 1.89$
27179 ♂	98	42	$\frac{98}{63} = 1.55$
27181 ♀	71	31	$\frac{71}{56} = 1.26$
Round Rock (*M. gregorii*)			
27200 ♂	195	70	$\frac{195}{97} = 2.01$

Some phytosaur skulls show peculiar features which I regard as abnormalities. Mehl's type skull of *Machaeroprosopus validus* was accompanied by a lower jaw which terminates beneath the sixth premaxillary tooth. In three specimens at hand the tip of the lower jaw lies just inside the two enlarged anterior premaxillary teeth, which appears to be the normal condition.

The rostrum of the type of *M. adamanensis* is turned upward rather sharply at the level of the eighteenth premaxillary tooth (fig. 10). The rostrum as imbedded rested across the mandible at this point and the curvature is probably due to

post-mortem pressure. If not, it is an abnormality, since other skulls do not show this feature in such a pronounced degree. There is in all skulls a slight upward slant of the anterior tooth row to allow the enlarged terminal teeth from below to close comfortably behind the premaxillary swelling.

New Species

The following supposedly distinct forms are described in the order of their stratigraphic occurrence. An outline of the principal characters by which they differ and the levels at which they are found has been given in table 2 on page 20. All type localities are in the Lower Chinle Triassic of northern Arizona.

Machaeroprosopus zunii n. sp.

Type.—Skull fragments with axial skeleton, parts of pelvis, fibula, portion of metapodial, and dermal scutes; U. C. Mus. Pal., no. 27036; found by C. L. Camp.

Type locality.—Three miles NE of St. Johns, Apache County, Arizona; lower St. Johns fossil horizon, 15 feet above the Chinle-Moenkopi contact. U. C. Mus. Pal., loc. 7307.

Diagnosis.—Rostrum very long, slender; nasals large, extending forward beyond nares and entering dorsal border of antorbital fenestra; posterior squamosal processes very large, broad, flat, and expanded vertically; parietals small, anterior suture lies well behind posterior border of orbits; posterior parietal processes Y-shaped; anterior border of supratemporal fenestra very wide and not excavated forward to or nearly to middle of parietals; postorbito-squamosal bar narrow. Skeletal differences as mentioned in the description of the type specimen may prove to be diagnostic, notably the character of the transverse processes of the tenth cervical vertebra.

Description of Type: *The skull.*—Fragments of the skull present in the type show the same, large broadened squamosal as indicated in other specimens from this and adjacent horizons. The nares are depressed and without elevated borders (♂).

Axis vertebra.—Suture between neural arch and centrum crosses below transverse process; transverse process relatively small, depressed; postzygapophyses relatively large.

Tenth cervical vertebra.—Rib facets on tip of transverse process set nearly perpendicular to axis of process, a very marked departure from the condition in *adamanensis.*

Eleventh cervical vertebra.—No groove in the anterior border of the transverse process.

Twelfth cervical vertebra.—Ventral border of diapophysis not close to edge of centrum.

Thirteenth to nineteenth vertebræ.—Dorsal tables on summits of neural spines are much less expanded and extensive than in *adamanensis.* The edges of these ovoid discs are thick and rounded, and do not overhang the posterior edge of the spine. There is a pronounced swelling on the posterior edge of the neural spines.

On vertebræ 13, 14, 15, and 16, the ventral diapophyses are nearly horizontal and the diapophyses are farther from the centrum than in *adamanensis.*

On vertebræ 13, 14, 15, and 16 the ventral diapophyses are nearly vertical and the diapophyses are closer to the centrum than in *zunii*.

On vertebræ 14 and 15 there is a sharp mid-ventral keel.

Twenty-fifth vertebra (last dorsal).—Oblique facets on posterior face are much more extensive than in *adamanensis*.

First sacral vertebra.—Spine same length as on last dorsal vertebra.

First caudal vertebra.—Postzygapophyses relatively smaller than in *adamanensis*, oval, and with no posterior notch; centrum not much bent in vertical plane and with posterior face more nearly on level with anterior face than in *adamanensis*.

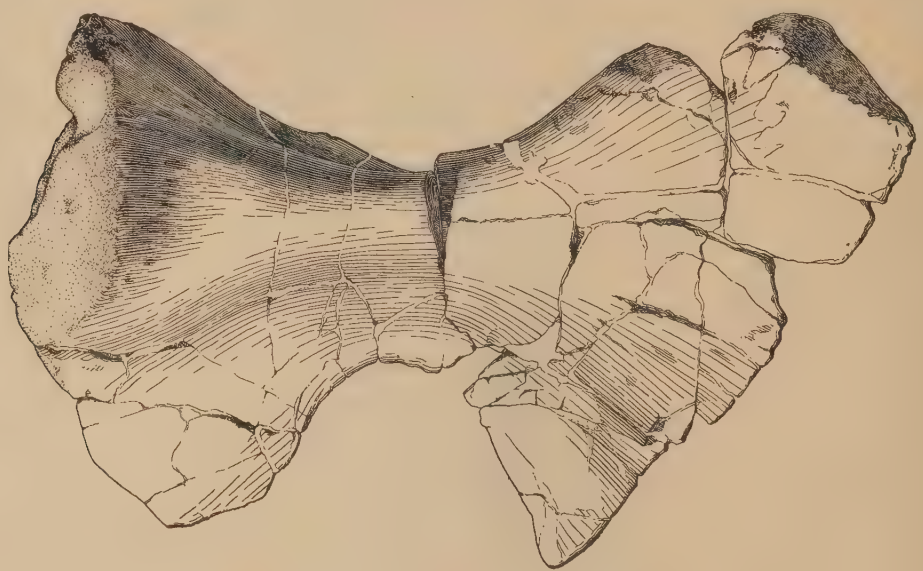


Fig. 7. Left ischium of *M. zunii* (type), 7307/27036, outer view, ×½.

Pelvis.—The ilium differs from *adamanensis* in having a lesser angle between the iliac crest and the anterior or pubic process of the ilium. The ischium (fig. 7) on the left side in the type skeleton is nearly complete, lacking only a small portion of the posterior extremity. There is a deep semicircular notch on the pubic border, half surrounding a large ischio-pubic fenestra which is partly closed below by the antero-ventral process of the ischium. It is likely that this fenestra was completely closed ventrally by symphyseal cartilage which doubtless extended from this process to the pubis. There is a smooth emargination in the ischial border of the pubis to accommodate the anterior margin of the fenestra. The ischial plate at the periphery of the fenestra is very thin making it appear that the fenestra has arisen to accommodate the obturator muscles.

When articulated with the ilium, the ischium projects nearly straight downward and the condition of the symphyseal border indicates no bony connection between the two ischia. The border is roughened however as if for a cartilage

across the symphysis. This separation of the ischia might be regarded as a female character. It seems more likely, however, that it is a specific difference. If it were a female character it would mean that the largest and most robust skulls are females.

The pubis is nearly complete on both sides. It resembles the pubis of *adamanensis* very closely. Its greatest length is slightly less than the crest of the ilium and the ilio-pubic angle is 50° rather than 55°, indicating that the pubis is more nearly vertical in *adamanensis* than in *zunii*.

The only element of the hind limb present in the type skeleton is a portion of the fibula. This is described on page 84.

Specimens referred to *M. zunii*.—All *Machaeroprosopus* material from the following localities in the vicinity of St. Johns, Arizona, is referred to this species (see map A): 7307 (upper and lower St. Johns), 7308 (Quarry), 7309 (Bone Flat), 7310 (upper and lower Peruvian), A 255 (Wild Bull). These localities lie less than fifty feet above the Chinle-Moenkopi contact. The principal bone-bearing localities 7307 and 7308 lie within twenty feet of this contact.

The following specimens from locality 7037, and from the exact stratigraphic level of the type are regarded as paratypes of this species: Lower St. Johns horizon—27041, tips of lower jaws with teeth; 27044, lower jaws 27048, portions of posterior part of skull; 27054, sacral vertebra; 27154, pubis; 27155, limb bones; 27156, head of large femur; 27189, fragments of skull and lower jaws.

The following specimens from the vicinity of St. Johns, Arizona, are from horizons lying within a few feet of the type horizon and are referred to this species: Upper St. Johns horizon—7307/27158, vertebræ; 7307/27159, disarticulated skull; Bone Flat horizon—7309/27056, small vertebræ; 7309/27057, large cervical vertebræ and ribs; Upper Peruvian—loc. 7310, fragmentary bones, scutes, and vertebræ; Wild Bull—loc. A 255, fragments.

Descriptions of specimens of *M. zunii*.—No complete skulls of this species are known, and there are no specimens present which show the character of the rostrum in its entire length. From sections at hand it is known to be attenuate without dorsal crests.

No. 27041 consists of fragments of a paratype lower jaw, weathered from a nodule. The swollen tips of the dentaries contain three enlarged teeth of which the third is the largest and the second nearly twice the diameter of the first. The next ten teeth are nearly of the same size. The spacing is wider than on specimens of *adamanensis* and *lithodendrorum* of comparable size.

No. 7044 is a large paratype lower jaw enclosed in a concretion. The symphyseal length is 600 mm. This is more than 160 mm. greater than in the largest specimens at hand of other species. The width of the tips of the dentaries and the widths at the symphysis on the other hand are about the same as in the type of *lithodendrorum*. This indicates that while this species, *zunii*, attained a size equal to or larger than that of *adamanensis*, *lithodendrorum*, and *gregorii*, the snout was much longer than in adults of any of these species.

No. 27048 consists of portions of a large paratype skull showing characters of the squamosal that appear to be peculiar to this species (fig. 3). The posterior extremity of this element is broadened into a thin, flat plate which is even higher in the vertical plane than in *adamanensis*. The bone is doubtless broadened in this way to accommodate enlarged cervical and pectoral muscles which have doubtless become developed to serve the elongate, cumbersome snout. While the ratio of length to height (1.17 : 1) is about the same as in *adamanensis* the area of bone surface on this specimen is much greater than in that species. This results in the absence of the entire post-ventral emargination. The anterior suture of the parietals lies about 10 mm. behind the posterior borders of the orbits. The posterior processes of the palatines are pointed and well separated, forming an inverted Y. The dorsal surface of the skull is roughened and sculptured into deep pits and irregular knobs and ridges (age character? [fig. 8]).

Fig. 8. Parietal region of *M. zunii*, 7307/27048, ×½.

No. 27189, paratype, consists of a few skull fragments and the anterior fourth of a pair of lower jaws found in a concretion. A portion of a right squamosal is slightly larger than in the preceding specimen and shows the same broadening in the vertical plane. The extensive area of bone developed below the posterior process extends posteriorly beyond this process and is even more greatly developed than in no. 27048.

The alveoli in the lower jaws are well spaced, despite the large size.

No. 27159 (fig. 9) is a partly dissociated skull with lower jaws, the anterior portions of which have weathered into fragments so small as to prevent restoration of the total length. The horizon is 10–20 feet above the type. The locality is about 100 yards from the type.

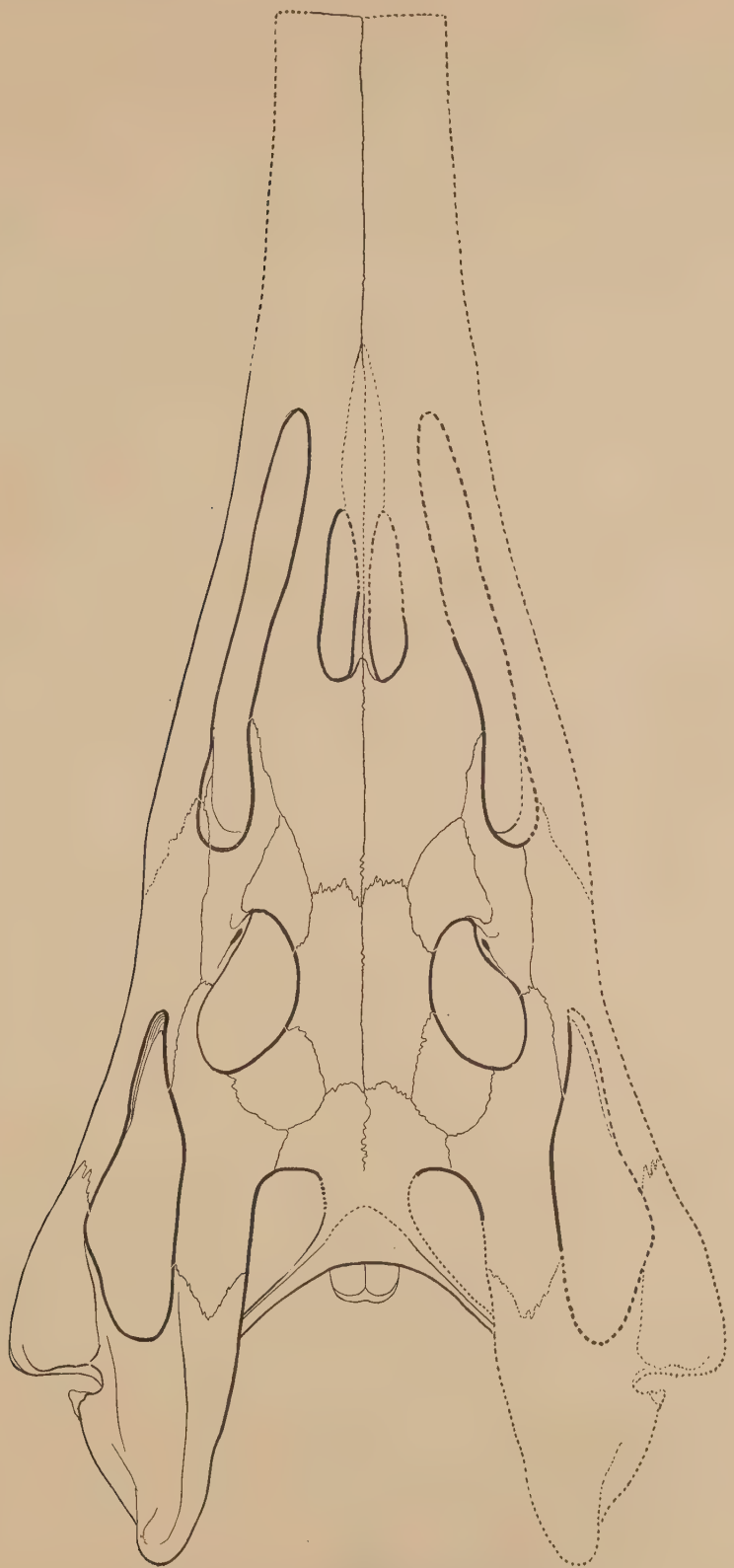


Fig. 9. Skull of *M. zunii*, 7307/27159, dorsal view, ×⅓.

This is a medium sized skull, considerably smaller than the type. The rostrum is slender; the nares depressed and without raised borders (♂); the surface of the bones roughened but not deeply so. The posterior maxillary alveoli are compressed and set closely but still retain the septa. The squamosal (fig. 3) is very thin and broadened in the vertical plane with the post-ventral emargination eliminated by growth of bone across it. This region has not grown backward quite so far as in the larger skulls just discussed; ratio of length to height 1.08 : 1. The parietals do not reach the level of the posterior margins of the orbits, and are very short. The orbits are much closer to the supratemporal fenestræ than to the nares. The postorbital bar is narrow and the supratemporal fenestræ are well exposed in dorsal view. The nares lie well behind the anterior margins of the antorbital fenestræ.

Machaeroprosopus adamanensis n. sp.

Type.—A skull (figs. 4, 10, 11; pls. 1, 2) with lower jaws (fig. 12), axial skeleton (pls. 3, 4), girdles (figs. 13–15) and dermal scutes (pl. 3); U. C. Mus. Pal., no. 26699; found by Miss Louise Kellogg.

Type locality.—Blue Forest, six miles SE of Adamana, in Apache County, Arizona; lower Blue Forest fossil horizon 209 feet above the base of the Chinle and Shinarump formations of the Triassic. U. C. Mus. Pal., loc. 7038.

Diagnosis.—Anterior part of rostrum slender in adults, with a slight mid-dorsal premaxillary swelling; two enlarged teeth on expanded tip of premaxillary; third and fourth teeth much smaller, directed obliquely outward with alveoli set out some distance buccally from rest of tooth row and separated from fifth tooth by a slight diastema; posterior premaxillary teeth slightly enlarged in adults; anterior maxillary teeth small, round, and fluted; posterior maxillary teeth enlarged, short, compressed, and serrate; 40–43 teeth on each side of upper jaws, 44–45 dentary teeth; alveoli separated by bony septa in adults, well spaced in young; posterior maxillary tooth just below or immediately posterior to posterior angle of antorbital fenestra; nasals large, extending forward beyond nares and touching border of antorbital fenestra; squamosals large, flat, and broadened in the vertical plane; ratio of length to height varies on three specimens from 1.15 : 1 to 1.28 : 1 (cf. fig. 3); parietals small, with anterior extremities at level of or behind a line tangent to the posterior borders of the orbits; posterior parietal processes Y-shaped; anterior border of supratemporal fenestra rounded and extending forward to or nearly to middle of parietals, leaving the antero-median border of the fenestra at the level of the skull top; postorbito-squamosal bar narrow, anterior process of palatines to or behind anterior border of internal nares.

Description of Type: *The skull* (figs. 10, 11; pls. 1, 2).—Total length 1095 mm., tip of snout to anterior end of nares, 618 mm., ratio of prenarial to narial-postnarial sections is 1.36 : 1 = 4 : 3. Snout with a short, well defined, rather sharp crest sloping gently from nares on a fairly straight line to a point above or just behind a plane passed vertically through the anterior limits of the maxillaries. Here an abrupt dip carries the crest down to the level of the slender portion of the rostrum. In the middle of the premaxillaries there is a very slight vertical swelling; 20 premaxillary and 21 maxillary teeth; nares elevated above posterior border of crest, with elevated borders and septum (♀?); anterior border of external nares about 40 mm. posterior to anterior point of internal nares; nasals forward far beyond antorbital fenestræ and meeting interior-dorsal border of same; septo-

maxillary extends forward to anterior border of nasals; greatest length of infratemporal fenestra, 185 mm., greatest width, 87 mm., ratio, 2.13; squamosal with ratio of length to breadth of 1.15 : 1; parieto-squamosal suture in middle of anterior border of supratemporal fenestra; anterior border of supratemporal fenestra cuts in to center of parietals; posterior palatine foramen and interpterygoid openings small; vomers flattened behind internal nares, extending forward on lower border of internarial septum and broadened again in front of nares; palatines extending forward only to anterior border of internal nares; palatal processes of premaxillaries do not reach internal nares; palatal portions of maxillaries from the external anterior borders of internal nares.

Axis vertebra.—In the type and also in another specimen (27025) from the same horizon, the suture between the neural arch and the centrum crosses below the transverse process; transverse process relatively depressed; postzygapophysis relatively large.

Tenth cervical vertebra.—Rib facet on tip of transverse process set at an angle to process, pointing downward and medially.

Eleventh cervical vertebra.—A very deep anterior groove in the transverse process.

Twelfth cervical vertebra.—Ventral border of diapophysis close to edge of centrum.

Thirteenth to nineteenth vertebræ.—Dorsal tables on summits of neural spines, for support of dermal armature, are very greatly expanded. The edges of these circular discs are thin, and overhang the posterior edge of the spine. There is no swelling on the posterior edge of the spines of these vertebræ.

The ventral surface of the centrum in vertebræ 14 and 15 is rounded.

Twenty-fifth vertebra (last dorsal).—Oblique facets on posterior face, for articulation with sacrum, are much less extensive than in *zunii*.

First sacral vertebra.—Spine longer than on last dorsal vertebra.

Fig. 10. Skull of type of *M. adamanensis*, 7038/26699, ×1/6, to show the upturned rostrum as it appears in the specimen. This feature appears to be due to crushing as it does not occur in other skulls. Absence of breakage at the flexure, however, may indicate that it represents the original condition in this individual. In other sketches of this skull the rostrum has been straightened.

First caudal vertebra (twenty-eighth).—Postzygapophysis relatively larger than in *zunii*, rounded, and with a posterior notch. Centrum bent, with posterior face much lower than anterior face.

Shoulder girdle.—Complete except for a portion of the interclavicle, the medial end of the right clavicle, and the left clavicle, which is missing.

The scapula and coracoid (fig. 14) are firmly ankylosed together on both sides. There is no material of *zunii* with which to compare this girdle.

All elements of the fore limb are missing in the type. The fore limb and girdle of *lithodendrorum* has not yet been prepared. The fore limbs and girdles are missing in the type of *zunii* with the doubtful exception of a portion of a right metacarpal of large size.

Pelvis.—The ilium (fig. 15) differs from the ilium of the type of *zunii* in having a wider angle between the dorsal and ventral moieties of the anterior border and in the relatively shorter posterior post-sacral extension.

The lessened angle between the anterior process of the iliac crest and the pubic process of the ilium appears to be a result of an elevation of the head of the pubis with respect to the acetabulum. This does not affect the inclination of the pubis. The plane of the ilio-pubic suture is the same in the two species. The dropping down of the head of the pubis in *zunii* may be to accommodate a larger abdominal space, hence possibly a sex difference. This might indicate that the type of *adamanensis* is a male and that of *zunii* a female. The nares are elevated in the former and depressed in the latter. Depression of the nares is seen on our largest and most robust skulls, consequently, as I have previously indicated, my supposition is that elevation of the nares is a female character. This may not be supported by the above facts concerning the ilium.

In support of the theory that the anterior iliac angle is a species difference, rather than a sex difference, attention should be directed to the fact that two other complete ilia (26730 and 27008) which are cotypes of *adamanensis* differ from *zunii* in the same way that the type does. In one of these (27008), a skull is present in which the nares are depressed.

The ischium in the type is about three-fourths complete on the left side. Apparently an anterior notch for the accommodation of a large ischio-pubic fenestra was present as in *zunii*, but this cannot be determined with certainty. The symphyseal border is flat and beveled in such a way as to make it appear that the right and left ischia are joined for some distance along the symphysis. Total length about 230 mm.

The pubis is complete on the right side in the type. Its greatest length is equal to the length of the crest of the ilium. The angle (pubo-iliac angle) made by the intersection of lines drawn through (1) the anterior extremity and the anterior border of the iliac suture and (2) through the points of the crest of the ilium, is 55°.

The hind limb is entirely missing in the type of *adamanensis*. It is described in other specimens of this species.

The dermal scutes are well preserved in the type, and many of the mid-dorsal scutes lie in their normal position, overlapping and in union with the vertebral spines over which they lie (pl. 4). The dermal scutes in the types of *adamanensis*, *lithodendrorum*, and *zunii* are irregularly triangular in outline and are very similar. No attempt will be made at present to determine specific differences between them. Comparisons with other genera will be made subsequently.

Remarks upon paratypes and referred specimens of *M. adamanensis*.—All phytosaur material from the following localities, in the vicinity of Adamana, Arizona, is tentatively referred to this species (map B): 7038 (upper and lower Blue Forest horizons), 7039 and 7040 (Phytosaur Basin), 7041 (Pictograph Tank), 7046 (base of Point of Bluff), 7047 (base of Twin Buttes). These localities lie from 209 to 280 feet above the Chinle-Moenkopi contact (sections, fig. 1).

The following specimens from locality 7038 are regarded as paratypes of this species. They were obtained in exactly the same horizon as the type and from within a few feet to within a few hundred yards of the type: 26696, head of femur; 26697, two sacral vertebræ; 26698, right dentary and splenial; 26706, pair of small dentaries; 26717, humerus, ventral portions of scapulæ, and fragments of skeleton; 26718, large femur; 26720, dorsal scutes; 26725, femur, fragments of vertebræ, ilium, and scutes; 26727, vertebra; 26729, vertebræ; 26730, ilium; 26731, vertebræ; 26756, left dentary, anterior part; 27070, crushed skull; 27093, dissociated skull elements; 27094, humerus; 27104, very small dentary; 27106, fragments of skull and lower jaws.

The following specimens from horizons 26 to 71 feet above the level of the type are referred to this species: Upper Blue Forest horizon (loc. 7038)—27099, small rostrum. Phytosaur Basin—7039/27006, humerus, scapulæ, and fragments of skull (probably not belonging to one individual); 7040/27007 and 27008, skull, ribs, ilia, ischia, vertebræ, femora, tibiæ, part of fibula, tibiale, gastralia, and dermal scutes; 7040/27010, fragments of skull and lower jaws; 7040(?), section of lower jaws. Pictograph Tank (loc. 7041)—27011, small crushed skull; 27013–15, skeletal fragments and teeth. There is some doubt as to the level of this horizon. Base of Point of Bluff—7046/27025, series of 13 cervical and dorsal vertebræ. Base of Twin Buttes (loc. 7047)—27026, large anterior dentary tooth; 27027, distal end of ulna.

Comparison of these specimens with the type so far as the material will permit discloses no pronounced differences in form of skull, number of teeth, and form of cervical and sacral vertebræ. There is accordingly some justification for our present view that all phytosaur remains so far recovered from these horizons in the vicinity of the Blue Forest may be referred to this one species. The skeleton of the lower extremities, missing on the type, is represented in other individuals, and the lower limb is present in a specimen (27007–27008) which includes much of the rest of the skeleton and the skull. The limb elements in this specimen are similar to scattered elements found in the same horizon as the type.

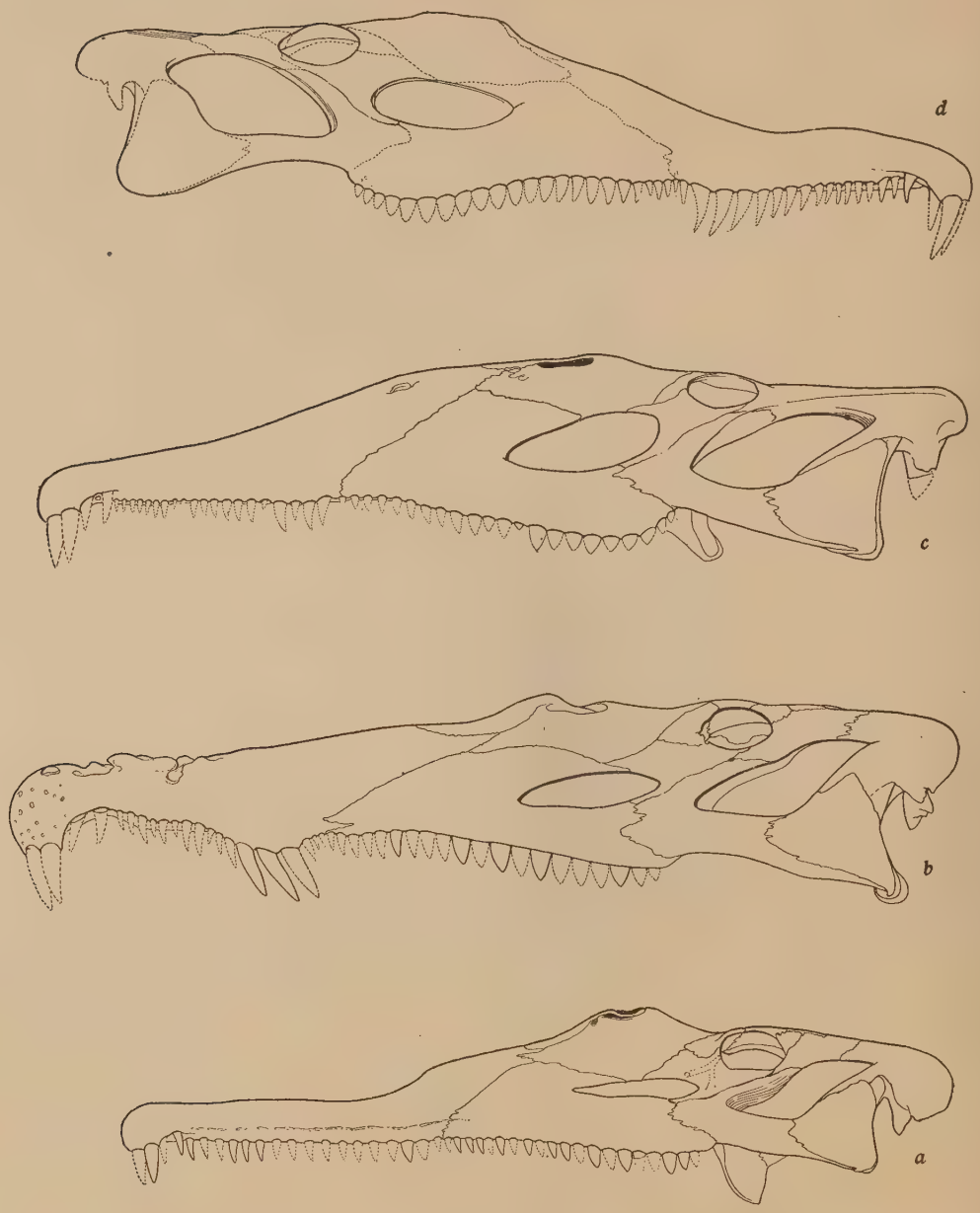


Fig. 11. Adult *Machaeroprosopus* skulls of four species, ×1/9.

a. M. adamanensis (type), 7038/26699.

b. M. gregorii, (type), A270/27200.

c. M. lithodendrorum (type), 7034/26688.

d. M. tenuis A257/27149.

DESCRIPTION OF SKULLS OF *M. adamanensis*.—No. 27070 is a paratype skull which has been crushed out flat and separated along the mid-line sutures. The rostrum on the left side and many of the dorsal skull elements are intact. The form of the rostrum is almost as in the type but the mid-premaxillary hump is a little more extensive and pronounced and, the specimen being somewhat smaller, the rostrum is a little more slender than in the type, and the crest does not extend so far forward.

There are 20 premaxillary and 23 maxillary teeth. The teeth are well spaced, not so greatly enlarged on the posterior end of the premaxillary as in the type. They are enlarged and flattened on the posterior portion of the maxillary. There are two enlarged teeth on the expanded tip of the premaxillary; fourth tooth equal to third in size; narial hump not prominent, nares without elevated rim (♂?); the nasals extend forward beyond the nares; squamosals vertically broadened very similar to those of the type; anterior point of parietals lies at level of posterior angle of orbits; anterior border of supratemporal fenestra very wide and extending not quite to middle of parietals; posterior tips of parietals slightly more separated than in type; lateral wing of parietals reaches beyond middle of anterior border of supra-temporal fenestra. Associated with this skull is a squamosal tip of another individual, which is extremely like the squamosals of this specimen.

No. 27093 is a small paratype skull represented by a number of dissociated dorsal skull elements, found within a few feet of specimen 27070. The prefrontals have a more pronounced orbital ridge than in the type and 27070. The parietals are similar to those of 27070.

No. 27006 includes a slender rostrum preserved in broken fragments in a hard, calcareous nodule. There are no distinctive characters except for the presence of two enlarged teeth on the expanded tips of the premaxillaries. The specimen is the largest yet discovered in the Adamana region.

No. 27007 (fig. 11) includes a skull and lower jaws which were very likely somewhat rotted before fossilization and have become softened and partly destroyed by the deposition of a crust of gypsum. The horizon is about 51 feet above that of the type. Portions of a skeleton (27008) were found near this skull, and seem to belong with it. The skull is nearly complete on the left side except for a mid-section through the maxillary-premaxillary suture. In figure 11 a terminal tooth which is present on the right side has been reversed in order to show it on the left.

The rostrum has much the same profile as the type but the mid-dorsal hump on the premaxillaries is somewhat larger, and the point of the rostral crest has not yet grown forward to lie above the anterior ends of the maxillaries, as it does in the type. The rostral crest is narrow as in all known members of this species but this is much accentuated by crushing. It is estimated that about thirteen teeth are missing from the gap in the maxillaries. This leaves a gap of 45 mm. or more in the dorsal line of the rostrum, giving a total length of approximately 950 mm. Of this, 380 mm. are included in the narial-postnarial length, giving a

prenarial-postnarial ratio of 3 : 2. There are 21 premaxillary teeth, two of which are enlarged and occupy the expanded tip of each premaxillary: teeth well spaced; posterior maxillary teeth much compressed; posterior premaxillary teeth slightly enlarged; last maxillary tooth lies just below posterior border of antorbital fenestra; no narial hump; nares without elevated borders (♂?); squamosal slightly more elongate and narrower than type, ratio of length to breadth 1.28 : 1; greatest length of infratemporal fenestra ±150 mm., greatest width 63 mm., ratio 2.38; anterior border of parietals forward to a line joining the posterior borders of orbits; lateral wing of parietals to edge of squamosal bar; anterior border of supratemporal fenestra wide and squarish, deeply excavating the parietals.

No. 27010 consists of fragments of a skull and lower jaws somewhat smaller than the type. The nares are not elevated and the teeth are widely spaced.

No. 27011 from one mile east of the Blue Forest, is a small skull, the posterior part of which is badly broken. The horizon is somewhat questionable but apparently a little below the lower Blue Forest. The sutures of the rostrum are separated indicating a young individual. The rostrum is very short and stout for such a small specimen, the sinuous outline is already developed, and the point of the crest is carried forward to a point above the anterior limits of the maxillaries, as in the type. A premaxillary hump is already present and is partly joined with the posterior crest. There are 19 teeth on the premaxillary, the two anterior ones being enlarged, the third and fourth of equal size, laterally placed and separated by a short diastema from the rest of the tooth row, as usual in this group of species. The posterior five or six premaxillary teeth are somewhat enlarged. The teeth are well spaced. The squamosal is broad in the vertical plane. The parietals extend forward to a line joining the posterior borders of the orbits. The border of the nares are not elevated (♂?).

Nos. 27013–15 are fragments of skulls and other bones which were found with 27011 but do not belong to that specimen. Included is the right maxillary of a skull much larger than the type and two broad squamosals resembling those of the type and belonging to two individuals.

No. 26698 is the symphyseal portion of a small dentary and splenial containing 33 teeth opposite the symphysis. The length of the symphysis is 358 mm. and the height at the posterior end of the symphysis is 50 mm., giving a ratio of length to height of 7.2 : 1. In the type there are 31–33 teeth opposite the symphysis and the ratio as given above is 7.1 : 1. The teeth are widely spaced except the small teeth just behind the anterior swelling which as usual are close together.

No. 27104 is the anterior portion of a very small dentary in which there are the alveoli of 23 well spaced teeth. As in the type the three teeth in the terminal expansion are enlarged, the third being the largest and the first the smallest. Further remarks on this tiny jaw may be found on page 26.

No. 26756, the anterior portion of a small left dentary shows perfectly the relations of the alveoli of the anterior teeth. The third tooth is more than twice as large as the first, and is the largest tooth in the skull. The fourth tooth is the

smallest tooth in the lower jaw and the next five are not much larger. A replacing tooth present in the eighth alveolus is very slender and slightly fluted. The terminal expansion of the dentary is flattened below, slopes upward to the septum between the second and third alveoli, and downward from there to the tip, which is below the level of the main tooth row.

No. 27106 includes the left articulare and surangulare of a lower jaw of nearly the same size as the type. The lateral ridge on the surangulare is not so high as in the type; otherwise the elements are very similar.

Machaeroprosopus gregorii n. sp.[3]

TYPE.—A skull (fig. 4 and pls. 5, 6) with lower jaws, eight associated vertebræ, a femur, and three dermal scutes; U. C. Mus. Pal., no. 27200; found by C. L. Camp.

TYPE LOCALITY.—Six miles SW of Round Rock trading post and three miles SE of Round Rock in northern Apache County, Arizona; upper portion of the Lower Chinle beds of the Triassic; horizon estimated to be 300 feet above the base of the Chinle. U. C. Mus. Pal., loc. A272.

DIAGNOSIS.—Anterior part of rostrum very heavy and massive, with mid-dorsal premaxillary swelling enlarged and joined to posterior portion of crest; two enlarged teeth on expanded tip of premaxillary; third and fourth teeth as in *adamanensis;* three posterior premaxillary teeth (except last three) abruptly and very greatly enlarged causing a swelling of the premaxillary in this region and a considerable depression of the alveolar border of the bone; maxillary teeth as in *adamanensis;* 41 teeth above, 47–48 below; alveoli crowded but retaining septa; posterior maxillary tooth lies just below posterior angle of antorbital fenestra; nasals as in *adamanensis;* squamosals narrower at tip than in *zunii*, broader than in *lithodendrorum*, *tenuis*, and *validus*, similar to *adamanensis* in form but thicker and not relatively so large, ratio of length to height 1.06–1.08 : 1; parietals very small, with anterior borders well behind level of orbits; anterior borders of supratemporal fenestræ reach middle of parietals, separated widely by broad Y-shaped posterior borders of parietals; anterior process of palatines to just behind anterior borders of choanæ; palatal processes of premaxillaries separate anterior borders of choanæ.

DESCRIPTION OF TYPE: *The skull* (fig. 4 and pls. 5, 6).—Total length 1230 mm., tip of snout to anterior borders of nares 671 mm., ratio of prenarial to narial-postnarial sections = 6 : 5. Snout with a heavy, low rounded crest running forward and downward from nares to a point near the tip of the rostrum and joining the mid-premaxillary hump; 21 premaxillary and 21 maxillary teeth; rims of nares at level of skull top (♂?); anterior border of external nares about 40 mm. posterior to anterior points of choanæ; nasals forward beyond antorbital fenestræ and not meeting dorsal border of same; greatest length of infratemporal fenestra, 245 mm., greatest width 110 mm., ratio, 2.23; squamosal with ratio of length to breadth of 1.08 : 1; parieto-squamosal suture lies at outer corner of anterior border of supratemporal fenestra; latter reaches to center of parietal and separates conjoined posterior "shelf" of parietals; posterior palatine foramen small, circular; vomers as in *adamanensis* but covered more completely by premaxillaries anterior to choanæ.

Lower jaws with relatively short symphysis and with symphyseal portion of splenials abbreviated; 34 teeth opposite symphysis.

[3] Named for Professor William King Gregory.

Specimens referred to *M. gregorii.*—Specimens referred to this species include fragments of phytosaur skulls found in the lower levels of the bentonite beds in the vicinity of Lukachukai and Round Rock as follows: A 270 (Hogan Valley), six miles west of new Lukachukai trading post, Navajo Reservation, Arizona; at base of badland exposures in blue, gray, violet, and purple bentonite. A 270/27192, phytosaur squamosal with thickened lateral ridge and postero-ventral tubercle as in *gregorii.* A 270/27195, portions of skull, scutes, and limb bones of phytosaur from same horizon as 27192. Squamosals similar to 27192, rostral crest heavy and rounded anteriorly as in *gregorii.* The sutures on the brain case are more clearly shown on this specimen than on any other available to me.

Machaeroprosopus lithodendrorum n. sp.

Type.—A skull (fig. 4) with lower jaws (fig. 12), cervical vertebræ, ribs, limb bones and dermal scutes; U. C. Mus. Pal., no. 26688; found by Miss Annie M. Alexander.

Type locality.—Lithodendron (Carrizo) Creek, six miles NW of Adamana, in Navajo County, Arizona; lower Carrizo fossil horizon, 346 feet above the base of the Chinle and Shinarump formations of the Triassic. U. C. Mus. Pal., loc. 7034.

Diagnosis.—Anterior part of rostrum heavy in adults, with the mid-dorsal premaxillary swelling obliterated by enlargement of the high, elongated rostral crest; two enlarged teeth on tip of premaxillary; third tooth much smaller; third and fourth teeth as in *adamanensis;* posterior premaxillary teeth greatly enlarged in adults; 44–45 teeth on each side of upper jaw, 47–49 dentary teeth; alveoli crowded in adults, septa of alveoli tend to disappear; hindmost maxillary tooth in adults lies well in front of posterior border of antorbital fenestra; nasals large, extending far forward and touching border of antorbital fenestra; squamosal relatively small, elongate not greatly expanded in vertical plane, thick and rounded, ratio of length to breadth measured on four specimens varies from 1.43 : 1 to 1.74 : 1; parietals extending forward to just beyond orbits, posterior processes Y-shaped; anterior border of supratemporal fenestra wide and not reaching middle of parietals, not excavating parietals as deeply as in *adamanensis;* anterior process of palatines reaches just beyond anterior border of internal nares.

Description of type: *The skull* (fig. 4).—Total length 1215 mm., tip of snout to anterior end of nares 600 mm., ratio of prenarial to narial-postnarial sections is 1.19 : 1 = 6 : 5. Snout with a massive, elevated crest extending from the nares to the base of the terminal expansion of the premaxillaries. The nares are not elevated above the upper level of this crest and the borders and septum are not elevated (♂). External nares posterior to internal nares; nasals extensive; palate crushed. Greatest length of infratemporal fenestra, 246 mm., greatest width, 114 mm., ratio 2.15; squamosal with ratio of length to breadth of 1.74 : 1. There are 21 or 22 premaxillary teeth, 23 maxillary teeth, and 47–49 dentary teeth.

The length of the symphysis of the lower jaws is 425 mm. The height at the posterior end of the symphysis is about 70 mm. There are 33 teeth opposite the symphysis.

The axis vertebra.—Postzygapophysis about one-third to one-fourth smaller than in the types of *zunii* and *adamanensis.* Other parts of skeleton not yet prepared.

Remarks upon paratypes and referred specimens of *M. lithodendrorum*.—All phytosaur material from the following localities in the vicinity of Carrizo (Lithodendron) Wash, and the First and Second Petrified Forests is provisionally referred to this species (see maps A, B): 7034 (lower Carrizo), A 258 (Brown Pool), 7042 (lower Billings Gap), 7044 (First Forest), 7037 (Second Forest). These localities all lie from 335 to 346 feet above the Chinle-Moenkopi contact (see sections, fig. 1).

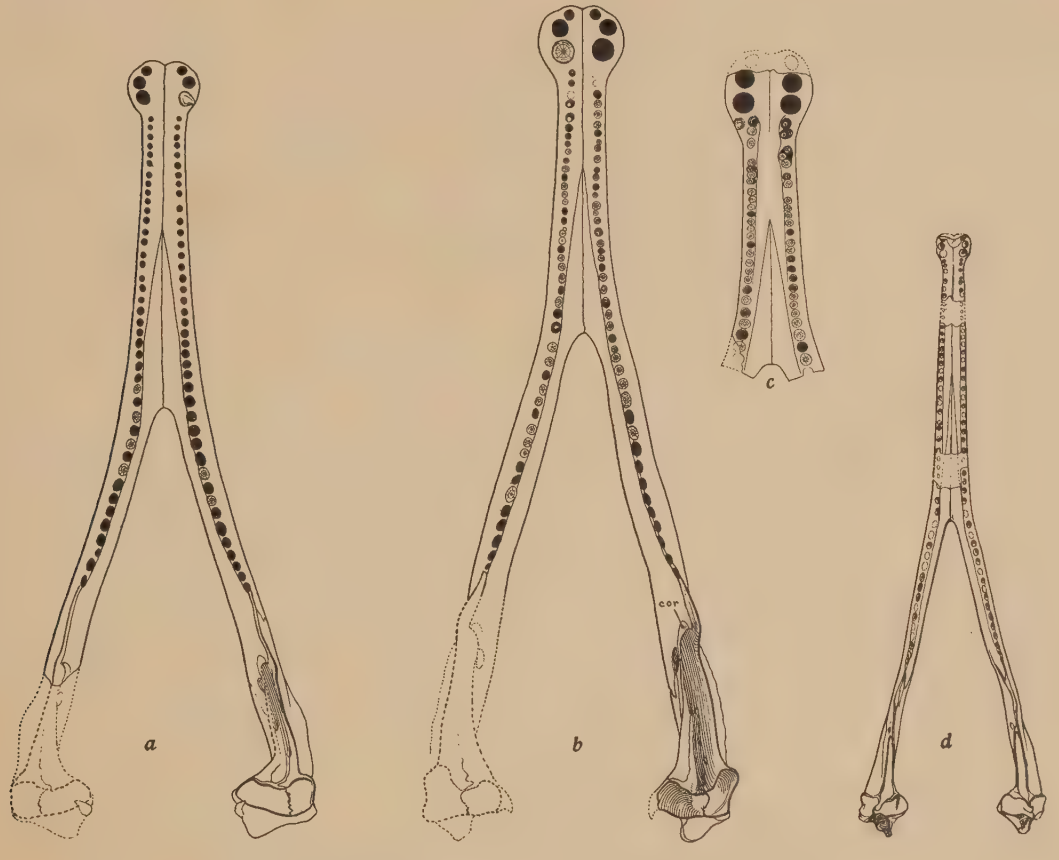


Fig. 12. Lower jaws of four species of *Machaeroprosopus*, ×1/9. *a. M. adamanensis* (type). *b. M. lithodendrorum* (type). *c. M. lithodendrorum* from specimen in geological collection of Northwestern University; collected eight miles south of Adamana, Arizona. *d. M. tenuis* (type).

The following specimens from locality 7034 in exactly the same horizon as the type and found within a quarter-mile radius of the type are regarded as paratypes of this species: 26683, fragments of large skull and dermal scutes; 26684, portion of small skull; 26719, skull lacking rostrum; 27179, small skull nearly complete; 27180, fragmentary skull; 27181, juvenile skull complete, with vertebræ and dermal scutes; 27182, large broken skull.

The following specimens from horizons eleven feet below up to the level of the type are referred to this species: Lower Carrizo horizon—A 258/27151, large

rostrum; Second Forest (loc. 7037, John Muir collection)—26693, squamosal and section of lower jaws; 26694, small lower jaws; loc. 7037*c*, limb bones; lower Billing's Gap—7042/27017, fragments of skeleton and scutes; 27183, tip of squamosal; 27184, squamosal; loc. A 256, three squamosals; A 257/27149, large skull, weathered on one side; loc. 7044, about 20 feet below the log zone in the First Forest—the symphyseal portion of a pair of lower jaws (in the geological collections of the Western Reserve University, Cleveland, Ohio).

The skulls of this species are of very diverse appearance, owing, I believe, to age differences. There is a uniformity in specific characters, and the small skulls are much alike in appearance with slender attenuated rostra and well spaced teeth. The largest skulls have heavy robust rostra and closely set teeth. It was at first thought probable that two species were represented here in the same horizon but there is the strong probability that the small skulls are the young of the one species. The skeleton is still imperfectly known; that of the type consists of crushed material much of which has not yet been prepared. The dermal scutes are similar to those of *M. adamanensis* and *zunii*.

Descriptions of skulls of *M. lithodendrorum*.—No. 26683 is a paratype skull found within a few feet of the type and weathered out of a thin lens of sandstone. As usual in specimens from sandstones, the bone is crusted with a thick covering of black iron oxide. The specimen is broken into fragments some of which fit together to form the anterior 220 mm. of the extremity of the rostrum, a mid-section of the rostrum, the fronto-parietal region, the occipital region, parts of the maxillaries, and two sections of the lower jaws. The rostral crest is high and massive extending forward as in the type to the expanded tips of the premaxillaries. The teeth are crowded and the external margins of the inter-alveolar septa are in places obliterated. The two enlarged anterior teeth are followed by a very long diastema, the surface bone having completely overgrown the roots and alveoli of the third, fourth, fifth, and possibly the sixth and seventh teeth. In cross-sections of the fourth and fifth teeth the truncated tooth roots may still be seen in the old alveoli, but there is no sign of them on the surface. This character may be associated with old age or perhaps the abrasion of the terminal teeth. This is the largest specimen of this species so far obtained. The anterior points of the parietals lie well in front of a line joining the posterior borders of the orbits. The dermal scutes are similar to those of the type.

No. 26719 (figs. 11, 16) is a well preserved skull, darkened and slightly encrusted with iron, which makes some of the sutures indeterminable. The posterior rostral crest is similar in shape to the type, but, this being a younger skull, the point of the crest lies a little behind the anterior limits of the maxillary. The rostrum is broken away across the middle of the premaxillaries leaving only a suggestion of a premaxillary hump. A very rough estimate would place the total length at ±965 mm. The postnarial distance is 399 mm. giving a pre-postnarial ratio of ±4 : 3. The posterior premaxillary teeth are enlarged and there are only 20 maxillary alveoli on the left side; alveoli well spaced; hindmost maxillary tooth

lies immediately below posterior angle of antorbital fenestra; nares depressed to level of crest, without raised borders on elevated septum (♂?); anterior border of external nares about 10 mm. posterior to internal nares; nasals forward to just beyond the antorbital fenestræ; septo-maxillaries very large, extending forward beyond nasals; squamosals very similar to type; ratio of length to breadth 1.19 : 1; greatest length of infratemporal fenestra, 156 mm., greatest width, 64, ratio 2.33; anterior suture of parietals forward to line joining posterior borders of orbits; anterior border of supratemporal fenestra wide and excavating parietals not quite to middle of parietals; anterior extremities of palatines lie posterior to anterior borders of internal nares.

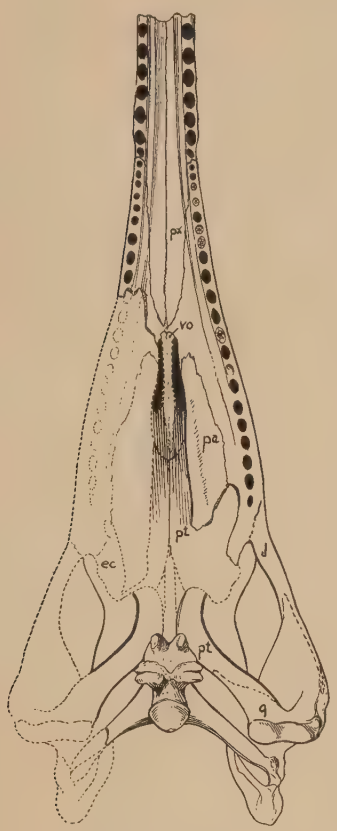


Fig. 13. Palate of *M. lithodendrorum* 7034/26719, ×1/6. See figs. 2*a* and 4*c* for other views of this specimen.

No. 27179 (fig. 5) is a small paratype skull found by Mr. Dick Grigsby of Adamana. It had settled upside down, doubtless in quiet water, upon the surface of a lens of soft white sandstone in the "fossil garden" about one-fourth of a mile east of the type specimen. The fragments now fitted together furnish a nearly complete skull which lacks the lower occipital and quadrate regions and a part of the left squamosal. The latter had been broken off before fossilization. The bone is encrusted with a thin coating of black oxide which has not been removed.

The total length is ±815 mm., of which 510 mm. is the prenarial length on the right side. This gives a pre-postnarial ratio of 1.67 : 1 or 5 : 3. The rostrum is very slender and without any suggestion of a median premaxillary hump. The nasal crest is carried down to the level of the slender premaxillaries at a point immediately above the anterior extremities of the maxillary. This small crest rises in a broad curve slightly above the level of the nares and has no break in its curvature until it reaches the cylindrical portion of the rostrum: There are 23 premaxillary teeth on each side, 22 maxillary teeth on the right side and 23 on the left. The posterior premaxillary teeth are very slightly enlarged, the anterior maxillary teeth are small. There are two enlarged terminal teeth followed by two laterally placed slightly smaller teeth and no diastema. The teeth are well spaced. The nares are depressed and without elevated borders (♂?). The anterior border of the right external naris lies slightly in front of the anterior borders of the internal nares (juvenile character?). The nares lie with their anterior borders above the anterior border of the antorbital fenestra. The nasals are extensive, extending far forward beyond the antorbital fenestræ and entering the dorsal borders of these fenestræ. The greatest length of the antorbital fenestra is 95 mm., the

greatest width, 40 mm., giving a ratio of 2.38 : 1. The squamosal is small and apparently not expanded vertically. The anterior suture of the parietals lies in front of the rear of the orbits; parietosquamosal suture at outer edge of anterior border of supratemporal fenestra; anterior border of supratemporal fenestra only slightly excavated in parietals; posterior palatine foramen large (7 mm. in width); palatines forward to beyond anterior border of internal nares; posterior palatal processes of premaxillaries reach internal nares.

No. 27181 (fig. 5) is a very small, juvenile, paratype skull entirely perfect on the left side and accompanied by numerous scutes and vertebræ. It was found in the "fossil garden" of the Carrizo about one hundred meters south of the preceding specimen (27179) and in exactly the same horizon as that specimen. This horizon is within ten feet of the level of the type specimen. The specimen lay on its side in a lens of soft white sandstone and rested on a thin surface of brown clay traversed by fossil mud cracks. Appearances point to a delta or shallow lake deposit. The rostrum has been crushed apart along the whole length of the mid-line suture.

The total length is 678 mm., the prenarial length 419 mm. and the pre-postnarial ratio 1.62 : 1 or nearly 5 : 3. The rostrum is very delicate and attenuated with no trace of a mid-premaxillary hump and with only a rudimentary posterior crest. This crest slopes down sharply from the nares to a point above the second and third anterior maxillary teeth. The teeth on the left side only have been counted. There are 24 premaxillary teeth and 21 or 22 maxillary teeth. The posterior premaxillary teeth are not enlarged, there are two enlarged teeth on the expanded tips of the premaxillaries, followed by the third and fourth fairly large laterally placed teeth, and no diastema. The tooth in the space occupied by a diastema in older specimens and in other species has not yet moved back against its neighbor. All this agrees with the conditions in the preceding specimen. The anterior maxillary teeth are smaller than those on the premaxillary. The alveoli of all the anterior teeth are very small and widely spaced. The nares are elevated and have raised borders and septum (♀). The anterior border of the external nares lies about 20 mm. in front of the internal nares (juvenile character), and 10 mm. in front of the anterior border of the antorbital fenestra. The nasals extend forward about 25 mm. beyond the nares, and the septomaxillaries appear to be large, extending forward at least as far as the nares. The antorbital fenestra is very small (juvenile character), its length is 70 mm. and its width 30 mm., giving a ratio of 2.33 : 1. The infratemporal fenestra is 94 mm. in greatest length, and 42 in greatest width, giving a ratio of 2.24 : 1. The squamosal is small and narrow in the vertical plane, its ratio of length to height being 1.49 : 1. The anterior sutures of the parietals lie well in front of the posterior borders of the orbits; the parieto-squamosal suture lies at the outer corner of the anterior border of the supratemporal fenestra; the latter cuts in only to about one-fourth of the length of the parietals; there is a small pit in middle of the inter-parietal suture which

probably marks the last vestige of an aperture for the parietal organ. This pit is in a symmetrical, slightly elevated portion of the parietal bones. It has never been found in adult phytosaurs.

No. 27182 is the posterior portion of a large paratype skull pieced together from surface fragments found a few feet from 27179 in the Carrizo. The horizon is exactly the same as for this latter specimen and is within ten feet of the level of the type. The skull had settled upside down and the elements which can be fitted together comprise the entire skull roof from the tip of the left squamosal to a point on the rostral crest about 230 mm. in front of the nares. The specimen is thickly coated with iron so that the sutures are almost entirely indistinguishable. The posterior rostral crest is massive and rounded as in the type and is of very peculiar profile. The nares terminate anteriorly in a high, rounded hump which dips forward into a saddle below the level of the nares and rises again to form an arched ridge which is thick, massive, and much roughened dorsally. The alveoli are separated by very narrow septa. The nares are very large, not elevated (♂?), and without raised borders. The squamosal is rounded, thick, pointed, and very long with respect to its height. Its ratio of length to height is about 1.43 : 1. The parietals extend forward to or just beyond the anterior borders of the orbits. The supratemporal fenestra penetrates the parietals only slightly.

No. 26684 includes a mid-section of a rostrum and a few broken fragments of a small skull (paratype ?), also a dermal scute. The exact horizon is not known. This specimen is encrusted in the same manner as 27182. The rostrum is slender. The posterior crest begins in an elevated knob just in front of the nares (as in 27182) and elevated above the level of the nares. The crest slopes down to the level of the slender premaxillaries just above the first maxillary tooth. The nares are depressed and without elevated borders (♂). The first five teeth are very small, the posterior five premaxillary teeth are somewhat enlarged.

No. 27151 is a massive rostrum slightly larger than that of the type. It was found, broken into sections, together with some scutes and parts of the lower jaws, and recently washed into a clay bank in a rivulet. Its horizon is almost the same as that of the type in a locality about a mile south of that of the type. The entire dorsal length of the premaxillaries is preserved as well as a short section of the anterior portion of the maxillaries. The crest is swollen, heavy, roughened, and rounded. In profile it is not quite so symmetrical as the type and appears to rise slightly from in front of the nares to a point just above the sixth maxillary alveolus. Here it starts to descend gradually to a point above the front of the posterior premaxillary alveolar swellings (seventeenth or eighteenth premaxillary tooth). From here it proceeds as a high, massive ridge as far as the base of the enlarged tip of the rostrum.

The form is very similar to the type the differences being chiefly the more sinuous profile and the more pronounced posterior premaxillary alveolar swellings. The greatly enlarged teeth in this region have carried the alveolar borders down

below the general level of the tooth row, even farther than in the type, giving the same kind of irregular border to the mouth as is seen in old crocodiles. Only 20 crowded alveoli can now be counted in the premaxillary. Some have doubtless become obliterated.

No. 26693 is an elongate squamosal whose ratio of length to height is 1.36 : 1. It is intermediate in character between *adamanensis* and *lithodendrorum*. The exact horizon is unknown. This number also includes many skeletal fragments associated with which is a section of a small lower jaw containing 19 very closely spaced alveoli. The fourth alveolus, lying just behind the enlarged third tooth, is larger than the fifth. In *adamanensis* this alveolus is smaller than the fifth. In *lithodendrorum* this alveolus is larger than the fifth. In a specimen of *zunii* it is about the same size as the fifth.

A specimen from locality 7044 consisting of the symphyseal section of a pair of lower jaws (fig. 12) is now in the collections of the Western Reserve University, Cleveland, Ohio (cf. p. 12). The horizon is about six feet below that of the type skull of this species. The parts preserved are short and massive. The length of the symphysis is about 390 mm., the height at the posterior end, 65 mm., and the width across the posterior end, 120 mm. There are 32 very crowded teeth opposite the symphysis. As usual, the third of the three enlarged terminal teeth is the largest.

Machaeroprosopus tenuis n. sp.[4]

Type.—Skull and lower jaws nearly complete, with fragments of left scapulo-coracoid and two dermal scutes; no. 27018, U. C. Mus. Pal., loc. 7043; found by E. L. Furlong.

Type locality.—Six and three-fourths miles due SE of Adamana, in Apache County, Arizona, and about one and one-half miles east of the NE corner of the Petrified Forest National Monument; upper Billings Gap fossil horizon, 375 feet above the Chinle-Moenkopi contact, and 166 feet above the lower Blue Forest horizon (type locality of *M. adamanensis*).

Diagnosis.—Rostrum without elevated crests, but massive in the adult; a dorsal premaxillary hump in the adult, placed far forward; two enlarged teeth on tip of premaxillary; third tooth but slightly smaller and well separated from the fourth; third and fourth teeth laterally placed and separated by a diastema from the fifth; posterior premaxillary teeth enlarged; 42–45 teeth on upper jaw, 49–50 on lower; alveoli crowded in adults; hindmost maxillary tooth lies behind posterior border of antorbital fenestra; nasals as in *M. adamanensis;* squamosal very small and thick and pointed, ratio of length to breadth varies from 1.75 : 1 to 2.07 : 1; postorbito-squamosal bar about twice as broad as in *M. lithodendrorum;* parietals extending forward to orbits, posterior processes joined across the mid-line; anterior border of supratemporal fenestra very narrow and but slightly excavated into parietals; owing to broadening of the postorbital bar, the parieto-postorbital suture intersects the outer edge of the supratemporal notch; palate as in the other species of *Machaeroprosopus* but, with anterior process of palatines, reaches beyond anterior border of internal nares.

Description of type: *The skull* (figs. 11 and 16).—Apparently a young individual of about the same size and stage of development as 27179 (*M. lithoden-*

[4] It is possible that the skull recently described by Mehl (1928*b*) from near Adamana under the name of *Pseudopalatus pristinus* belongs to this species.

drorum) but entirely lacking the posterior rostral crest, with even more pointed squamosals than in *lithodendrorum*, and with the postorbito-squamosal bar twice the breadth of any comparable specimens of *lithodendrorum* and *adamanensis*.

The specimen was discovered in place, resting dorsal side up in a bed of brownish purple, shaly sandstone. The lower jaws were still in articulation with the skull. The tips of both lower and upper jaws had been weathered away but were for the most part recovered, so that the total length could be ascertained. The bone was coated with a thin, hard shell of brown oxide, which has been removed revealing the open sutures of an apparently juvenile specimen.

The total length is 819 mm., of which 513 mm. is prenarial, giving a pre-postnarial ratio of 1.68 : 1 or 5 : 3. The rostrum is very slender, without any trace of a mid-dorsal premaxillary hump. The posterior crest is absent, the profile being carried down abruptly from the nares to the level of the slender premaxillaries to a point above the fifth maxillary tooth. There are 21 maxillary teeth on each side. It is estimated that there were 24 teeth on the premaxillary. The lower jaw carries 49 or 50 teeth. The teeth are widely spaced and the posterior premaxillary teeth are slightly enlarged. The nares are elevated with slightly raised borders and septum (♀). The anterior borders of the external nares lie immediately above the anterior borders of the internal nares. The position of the anterior border of the antorbital fenestra is doubtful, but it was certainly not much if any distance in advance of the anterior borders of the nares. The nasals are extensive, extending 60 mm. anterior to the nares, and the septomaxillaries run forward as thin medial bars to the same distance. The antorbital fenestra, as in other young individuals, is small. The infratemporal fenestra measures 132 mm.×64 mm., giving a ratio of height to width of 2.06 : 1. The squamosal is small, elongate, thick, and pointed, with a ratio of height to length of 2.07 : 1. Its dorsal border is turned inward to form a broad horizontal surface. Four other small squamosals found in this vicinity and in the same horizon as this specimen are all similar in shape and proportions. The anterior sutures of the parietals lie in front of a line joining the posterior borders of the orbits; parietosquamosal suture at outer edge of anterior border of supratemporal fenestra; the latter very narrow, and only slightly excavates the broad posterior margins of the parietals; palatines forward to beyond anterior borders of internal nares; posterior processes of parietals joined into a broad flat plate.

Specimens referred to *M. tenuis*.—The horizon of the type lies about thirty feet above the type horizon of *M. lithodendrorum*. The horizons of the two species are separated, however, not by shale beds alone but by extensive sandstone lenses in which the fossil logs of the First and Second Forests occur. Specimens from the following localities are referred to this species: 7043 (upper Billing's Gap), A 256 (Limestone Reef), A 257 (Cowboy), 7036 (upper Carrizo unidentifiable fragments of a rostrum), 7050 (White Hills).

Descriptions of skulls of *M. tenuis*.—No. 27149 is a large skull (fig. 4), found near Billing's Gap about one mile west of the type specimen, and within

ten feet of the same horizon as the type. The specimen was in place, lying on its right side in a soft, coarse sandstone containing small irregular chunks of purple bentonite. A part of the left maxillary, the left squamosal, the quadrate, and quadratojugal are weathered away.

This skull differs in form from any yet discovered, these differences appearing mainly in the dorsal contour. The rostrum is heavy, but without a prominent dorsal crest. There is a dorsal premaxillary hump placed far forward above the seventh to eleventh premaxillary teeth. The dorsal line above the twelfth to the sixteenth alveoli is depressed and rises gradually from that point to a point above the ninth maxillary tooth where it inclines more sharply to the narial protuberance.

The total length is about 1194 mm., of which 644 mm. is prenarial, giving a ratio of 1.17 : 1 or 8 : 7. There are only 19 premaxillary teeth which are so crowded that many of the inter-alveolar septa have disappeared. The posterior 5 premaxillary teeth are greatly enlarged except the last tooth which is smaller. There is a diastema between the third and fourth teeth, which as usual are placed laterally on the rostrum, and the fourth tooth is separated from the small fifth tooth by a second diastema. There are two, much enlarged teeth on the swollen tip of the premaxillary, and the third is nearly as large. There were 23 teeth on the right maxillary, those opposite the anterior maxillary constriction being small and round; those posterior were compressed and crowded. The hindmost maxillary tooth lies in front of the posterior border of the antorbital fenestra.

The nares are elevated on a prominent elliptical boss and have thick, elevated, rounded and roughened rims and septum (♀). The anterior borders lie behind the internal nares and behind the anterior border of the antorbital fenestra. The nasals extend far beyond the nares and the antorbital fenestra, to a point above the twelfth maxillary tooth. The antorbital fenestra is very large, measuring 180×85 mm. The infratemporal fenestra is so damaged that exact measurements cannot be secured but approximate dimensions are 220×120 mm., a ratio of 1.83 : 1. The squamosal is relatively very small, thick, and but little expanded in the vertical plane. Its ratio of length to breadth is approximately 1.75 : 1. Its dorsal border is turned inward as in the type. The postorbito-squamosal bar is much broader than in any other specimens in our collections. The parietal region is weathered beyond hope of recovery.

A large lower jaw, 7050/27031, nearly complete on the left side, comes from a locality in the "White Hills" on the Navajo-Hunt road, 18 miles due southeast of Adamana. The stratigraphic horizon is not known but is certainly rather high in the Lower Chinle, perhaps not far from the level of the upper Billing's Gap bone bed. The characters agree more closely with *tenuis* than with other known species. The symphysis is relatively long and the splenial portion of the symphysis much abbreviated. There are 36 alveoli opposite the symphysis.

Comparisons with Other Species of *Machaeroprosopus*

Two species of the genus *Machaeroprosopus* have been previously described and figured. These are: the type, *M. validus* Mehl (1916), and a very different skull from eastern New Mexico, *M. andersoni* Mehl (1922). In addition, the fragmentary skull-top from Texas, described as *Phytosaurus* (*Machaeroprosopus*) *doughtyi* Case (1920), and the New Mexican skull described as "*Belodon buceros*" Cope (1887) may also belong to this genus.

M. validus (type) is a short, stumpy skull from Tanner Crossing, Arizona. The locality lies in the Lower Chinle perhaps 200 feet above "the lithodendron member of the Shinarump Group of the Triassic." This places the horizon 600 to 700 feet above the top of the Moenkopi, and at least 200 feet above the highest fossil horizons at Adamana in which our phytosaur material has been collected.

M. validus differs very decidedly from *M. adamanensis*, *M. gregorii*, *M. lithodendrorum*, *M. tenuis*, and *M. zunii* in the following particulars: the skull is much shorter and more elevated, the height at the orbits being contained in the total length only about five times. In two of our species this height is contained six or more times in the total length.

The squamosal region is not extended so far posteriorly, the distance from the orbits to the tip of the squamosal being contained over five times in the total length. In two of our species this distance is contained four and one-half times into the total length.

There are only 37 teeth on each side of the upper jaw; 40–45 in four of our species. The posterior premaxillary teeth do not seem to be enlarged, and the anterior maxillary teeth are not reduced in size in *validus*. This may however be due to a misplacing of the maxillary-premaxillary suture on the figures. There are three, rather than two, enlarged teeth on the terminal expansion of the premaxillary.

The nasals are very small, not reaching the antorbital fenestra and extending forward only slightly beyond the nares.

The frontals are much shorter than in our specimens, being shorter than the parietals and nearly as broad as long.

The parietals are excavated only slightly by the anterior borders of the supratemporal fenestræ and the median posterior tips are much abbreviated and end on the mid-line in a short point.

The maxillary-premaxillary suture meets the tooth row at a point considerably behind the anterior extremities of the maxillaries. This may however be due to a misplacing of the suture in Mehl's figures.

There are only 39 or 40 teeth in the dentary. The second and third of these are nearly equal in size. In our species there are from 44 to 50 teeth in the dentary and the second tooth is considerably smaller than the third.

The lower jaw is much shorter than the upper in the type of *M. validus* but there is at least the possibility that it is pathological or that it may not belong to the skull described. In the types of *M. adamanensis, M. lithodendrorum,* and *M. gregorii* the lower jaws are only slightly shorter than the upper.

The lower jaws of *validus* are much stouter than in *adamanensis,* the greatest height being contained in the total length less than six times in the former and more than seven times in the latter. In a large adult (the type) of *lithodendrorum,* the height of the lower jaw is contained a little more than six times in the total length. In a young specimen (27018) of *tenuis* this dimension is contained more than seven times in the total length. In a specimen from Tanner Crossing referred by Mehl to *Angistorhinus,* this height is contained about seven times in the total length, and the teeth are ±42 in number. There are about 30 teeth opposite the symphysis in this specimen referred to *Angistorhinus.* In *M. validus* there are, according to Mehl's figures, about 28 such teeth. In our specimens there are from 32 to 37 such teeth (32 in the type of *adamanensis;* 33 in another specimen of the same species, 26698; 34 in the type of *lithodendrorum;* 34–35 in the type of *tenuis;* and 36 in a referred specimen of *tenuis,* 27031).

In our material the smaller jaws are more slender than the larger, indicating an increase in stockiness along with growth. Also there is a tendency to lose one or two alveoli in the older skulls. These facts lead me to regard the lower jaw, referred by Mehl (1916) to "*Angistorhinus?* sp." as probably belonging to a young individual of his species *validus.*

The total length of the type skull of *M. validus* as measured on Mehl's figures is 1062 mm., which is a little less than the largest skulls of the three species described in the present paper. Perhaps we might regard the shortening of this skull, the extreme depression of its supratemporal fenestræ, the development of a third enlarged anterior tooth, the lesser number of teeth, and the great size of the antorbital fenestræ as indicative of a specialization in advance of anything we find in our species from the lower levels of the southern Painted Desert area.

The species from Guadaloupe County, New Mexico, described as *Machaeroprosopus andersoni* by Mehl (1922), is of more slender proportions than *M. validus* and is a smaller, possibly a younger individual. The stratigraphic level of the find is unknown, but it is possibly from the upper part of the Dockum. The differences between this incomplete skull and our specimens are not so great as in the case of *M. validus.* They are as follows: no mid-dorsal hump on the premaxillaries; 47 teeth on right upper jaw and 48 on the left in Mehl's figure; the lateral expansion of the rostrum is more abrupt than in our species with the exception of *gregorii.* The palatines extend far in front of the internal nares. Unfortunately the squamosal region is not known. The postfrontals are less extensive; the nasals apparently do not enter the dorsal border of the antorbital fenestra, which is very small.

The resemblances between *andersoni* and our species *tenuis* are quite marked in the posterior region of the skull. Here the anterior border of the supratemporal

fenestra is narrow, as in *tenuis*, and the posterior extremities of the parietals are conjoined into a broad surface. The disposition of the parietal sutures is also similar.

The resemblances between the species *andersoni* and our species *adamanensis*, *lithodendrorum*, and *tenuis* include the disposition and size of the alveoli on the anterior extremity of the premaxillaries and the general form of the palate with its underarched palatines.

The skull fragments described as *Phytosaurus* (*Machaeroprosopus*) *doughtyi* by Case (1920) differ only slightly from our forms. The quadratojugal does not extend upward to the level of the inferior squamosal notch and is dovetailed into the squamosal in a way not shown in our species. The nasals are said not to "include or extend in front of the nares," perhaps a doubtful point. The nares are separated from the orbits by a distance greater than the diameter of the latter. The lacrimal surrounds the whole posterior border of the antorbital fenestra.

In view of certain resemblances between this skull and the various species of *Machaeroprosopus*, I feel that it may be doubtfully included in this genus. The weight of evidence against such a step is that the postnarial-orbital region is very long, and the squamosals are very widely separated from the mid-line much as in Cope's species *buceros*. This may indicate a broader-bodied form than *Machaeroprosopus*. On the other hand this feature may be due to crushing.

Cope's "*Belodon buceros*" is a skull which differs more widely from our forms than any previously discussed. In the first place it has all the earmarks of being a fully adult individual and is therefore a much smaller form than other known species of *Machaeroprosopus*. The rostral crest is high and roughened as in adults of our species *lithodendrorum*, which are of much greater size, and there is a ventrally projecting flange over the posterior premaxillary teeth. Furthermore, the teeth are somewhat crowded.

This skull differs from the known forms of *Machaeroprosopus* particularly in the following respects: both antorbital and lateral temporal openings very small for an adult skull; nares subcircular instead of compressed; supratemporal opening more depressed and not excavating the parietals; no posterior processes on the parietals; no posttemporal fenestra according to Huene's figure (1915, fig. 11*d*); the jugal-quadratojugal bar appears to be exceptionally slender. Since we know nothing of the length of the snout, the skeleton, or the dermal scutes of *buceros*, we should hesitate to assign it a place within any known genera despite some resemblances to *Machaeroprosopus* and even to *Phytosaurus*. The extreme depression of the supratemporal fenestra, which is not visible in dorsal view, apparently indicates a specialization beyond that of *Machaeroprosopus*. The wide separation of the tips of the squamosals, if not due to crushing, may indicate a broad-bodied form. It is possible, as Huene suggests, that this skull belongs to the genus *Typothorax*.

CHARACTERS OF THE GENUS *MACHAEROPROSOPUS* MEHL

We may now give a preliminary summary of the characters of the genus *Machaeroprosopus*.

The skull is similar to *Phytosaurus* but attains a much larger size. Most of the known skeletal characters differ from the surmised structures in *Phytosaurus;* some of the distinctive features of the skeleton being perhaps developed in correlation with more active terrestrial life than is indicated in other phytosaurs.

The following characters appear to be peculiar to this genus. While some latitude must be allowed for future discoveries, it is not likely that all of these will be overthrown:

1. Anterior border of external nares posterior to anterior border of internal nares. A specialized character. In a young skull the external nares lie slightly in advance of the internal.
2. Transverse produced ventrally into a very broad cardiform plate. Correlated with great size of lower jaw and enlargement of pterygoid muscles.
3. Spines of cervical vertebræ highly differentiated. A specialized character doubtless concerned with the great size and weight of the head.
4. Spines of anterior dorsal vertebræ with summits more broadly expanded than in other known forms.
5. Last two lumbar "ribs" with fused tuberculum and capitulum and united by suture to the transverse processes.
6. Three anterior caudal transverse processes occupy nearly whole width of centrum.
7. Sacral centra ankylosed.
8. Fourth trochanter of femur longer than in other known forms including *Typothorax*.
9. Tibia relatively longer than in other described forms.
10. Size attained appears to be greater than in other known forms.

COMPARISONS WITH OTHER GENERA OF PHYTOSAURS

GENERAL STATEMENTS

In studying the relationships of *Machaeroprosopus* to other phytosaurian genera, it will first be necessary to reexamine the status of the forms described from eastern North America.

Phytosaur remains have been described during the past seventy-eight years from the so-called Newark Triassic of the Atlantic coast from Connecticut to North Carolina. So many descriptions have been based upon scanty material—isolated teeth and skeletal parts—that the taxonomy is obscure. The only known skulls are those from North Carolina assigned to *Rutiodon carolinensis* (cf. McGregor, 1906).

These skulls and skeletal materials of *Rutiodon* have been considered as generically identical with certain more fragmentary remains from Pennsylvania, New Jersey, and Connecticut, of which descriptions and revisions have recently been

given by Huene (1913 and 1921), Lull (1915), and Sinclair (1918). I have not examined any of the specimens, but comparisons of figures, photographs, and descriptions make me feel confident that the type specimen of *"Rutiodon" manhattanensis* and the specimens referred to this species by Sinclair are more similar to *Machaeroprosopus* than to *Rutiodon*. This similarity is so close that generic identity of the northern Atlantic coast forms with *Machaeroprosopus* may well be expected. In absence of skull material of these it would not be wise, however, to assign the western material to any previously described eastern genus. For reasons detailed below, it is perhaps best at present to include all the large phytosaurs from Pennsylvania and New Jersey in the single genus *Clepsysaurus* Lea, which may be tentatively regarded as distinct from *Machaeroprosopus* with the probability that the two will be united should adequate material be discovered.

Comparisons of known characters of *Machaeroprosopus*, *Clepsysaurus*, and *Rutiodon*.

Machaeroprosopus adamanensis	*Clepsysaurus manhattanensis*	*Rutiodon carolinensis*
Eleven characters of the ilium as given in table 5, p. 77.	Similar in nine of these characters.	Similar in only three of these characters.
Width of head of femur enters length of femur 3½ to 4 times in three specimens.	Width of head of femur enters length of femur 3⅔ to 4 times in three specimens.	Width of head of femur enters length of femur over 4 times.
Pubic plate quadrilateral with long straight symphysis.	Pubic plate as in *Machaeroprosopus*.	Pubic plate subcircular and without elongate symphysis.
Spine of last presacral vertebra longer than height from base of centrum to upper edge of zygapophysis.	Same as in *Machaeroprosopus*.	Spine of last presacral shorter than height from base of centrum to zygapophysis.
Last presacral rib joined to transverse process by suture.	Last presacral rib as in *Machaeroprosopus*.	Last presacral rib free.

In view of the wide differences which exist among several western genera in the characters of the ilium, I regard these pelvic resemblances of *manhattanensis* to species of *Machaeroprosopus* as fair evidence of generic identity. It now remains to examine the teeth.

Sinclair states that the teeth accompanying his specimen of *manhattanensis* "combine characters distributed among various supposedly dinosaurian genera (*Palæoctonus, Clepsysaurus*) described . . . . from the Triassic of Phoenixville, Pennsylvania, and as there is every reason to believe that the teeth illustrated . . . . belong to a single individual, probably several of the Phoenixville dinosaurs are really Parasuchians and identical with *Rutiodon manhattanensis*."

I should concur in these views. The type skull of *Machaeroprosopus adamanensis* contains many of the teeth preserved *in situ*. The lower jaw of this specimen also retains one of the enlarged anterior teeth. There are in addition about 300 isolated teeth from the vicinity of Adamana which may be referred without much question to *adamanensis*, as well as many teeth from other localities and teeth in other skulls belonging to other species of *Machaeroprosopus*.

The teeth in place in the type skull of *adamanensis* show that the enlarged anterior premaxillary and dentary dentition was of the type figured by Huene (1921, fig. 2) and in the present paper (pl. 2). The tooth in Huene's figure is one of Cope's specimens of *Palæoctonus appalachianus*. It is almost an exact mirror image of the tooth on the right side of the tip of the lower jaw in the type of *adamanensis*. Therefore it must belong in the second or third alveolus of the left side of the lower jaw. The flatter side is the lingual side and the longer serrated edge is posterior in both upper and lower jaws. In the upper jaw the enlarged anterior teeth are straight; they are curved, as in Huene's figure, in the lower. Also, the lower teeth are slightly larger and stouter than the upper. Cope's specimen is a large one, one-third again as long as the type of *adamanensis*, but we have a corresponding tooth of another specimen of *adamanensis* which is a fourth again as large as Cope's. These teeth are, of course, much larger than in any known specimens of *Mystriosuchus* or of *Rutiodon carolinensis*, they are more highly differentiated, and are for the most part of different shape.

The middle premaxillary teeth of the type of *M. adamanensis* are slender, conical, sulcate, and of nearly circular cross-section. The anterior, smaller ones resemble the teeth figured by Huene (1921) as *Suchoprion sulcidens*. Those a little farther back (8th–12th) are more slender, with only faint traces of anterior and posterior serrations and of nearly circular section. In shape they resemble the teeth figured by Huene (1921) as *"Belodon" priscus* but they are sulcated and are provided with anterior serrations. We do have some loose teeth, however, which are duplicates of *priscus*.

The posterior premaxillary teeth are elongate, flattened on the inner side, and well equipped with anterior and posterior serrations. They resemble the teeth figured as *Palæoctonus aulacodus* by Huene (1921), fig. 4, *A*, *B*).

The anterior maxillary teeth of *M. adamanensis* are small, short, compressed, sulcated near the base, and provided with distinct anterior and posterior serrations (pl. 2). They are almost identical with Huene's first figures of *Palæoctonus aulacodus* (1921, fig. 3, *A*. *B*). These teeth grade backward into the type of teeth figured by Huene (fig. 1) as *Palæoctonus appalachianus*. The sulcations are lost on the seventh or eighth maxillary tooth, and the teeth increase in breadth and height and are more compressed near the posterior end of the maxillary than anywhere else on the upper jaw. The tendency is for these teeth to be constricted at the base.

A small section of a lower jaw of *adamanensis* (26756) contains a very slender, conical tooth just behind the enlarged anterior ones. Other teeth in our collections are of similar shape, slenderly conical and curved, with traces of sulcations and anterior and posterior serrations. These teeth are similar to *Clepsysaurus pennsylvanicus* as figured by Huene (1921) but are flatter on the lingual side and some of them are more sharply curved. These conical teeth grade posteriorly into triangular, compressed blades similar to posterior teeth on the upper jaw.

There is little doubt therefore that the various species of *Palœoctonus*, *Suchoprion*, *Clepsysaurus*, and probably *Palœosaurus fraserianus* and *Belodon priscus* as well, belong to a single genus, probably to a single species of phytosaur. This genus should take the oldest name, which is *Clepsysaurus*. As long as any doubt remains as to the identity of this genus and *Machaeroprosopus*, it may be well to retain the latter name for the Arizona forms.

There still remains a question as to the allocation of *Belodon validus* Marsh from the Connecticut sandstones. This species was *nomen nudum* until Marsh's specimen was described and figured by Lull (1915). Lull placed the species in the genus *Rutiodon* but recognized several points of difference between the fragment and *Rutiodon carolinensis*. These points are: element half again as large and more robust; groove on sutural surface of coracoid facet of scapula transverse rather than oblique; no roughening above glenoid facet; no fissure immediately behind glenoid facet. I should add that the triceps tubercle on the posterior border, about 7 cm. above the glenoid, is less pronounced than in *Rutiodon carolinensis*.

In *Machaeroprosopus adamanensis* there is a notch in front of and behind the glenoid, and the roughening for the origin of the teres minor above the glenoid is more pronounced than in Marsh's *validus* but less so than in *Rutiodon carolinensis*. In the other three points mentioned, Marsh's *validus* seems very close to, if not identical with, *Machaeroprosopus*. It was evidently a large, stout form with a strong, broad connection between coracoid and scapula and consequently was perhaps a more terrestrial form than *Rutiodon*.

It would seem best to assign *validus* tentatively to the genus *Clepsysaurus* which occurs in the same general series of beds and which also appears to differ very slightly if at all from *Machaeroprosopus*. This procedure renders it unnecessary at present to change the name of the type species of *Machaeroprosopus*, which Mehl described under the same name as Marsh's specimen (*validus*).

There now remains the difficult matter of comparing the various known phytosaur genera with a view to determining something of their relationships and the place of *Machaeroprosopus* in the scheme.

Our problem is complicated by the puzzling question as to what to do with such forms as *Phytosaurus kapffi* and *Machaeroprosopus lithodendrorum*, which have similar skulls but strikingly different skeletons. Does this mean an adaptive parallelism in skull structure in two different stocks, or does it indicate that the skull quickly reached a high adaptive level and remained comparatively unchanged while the skeleton of at least one of the groups continued to undergo modification? I hesitate to attempt an answer without being sure of the association of the skulls and the supposed skeletal parts of *Phytosaurus*.

There can, however, be little objection to the separation of all the American genera from those of Europe. Altogether there is skull material representing six genera of the former and four of the latter and enough associated skeletal material to make the case fairly sound. Data for further comparison of genera will now be considered.

THE SKULL

Our material shows that a pronounced shortening of the relative length of the rostrum accompanies growth in *Machaeroprosopus*. This makes some previous generic comparisons based on the pre-postnarial ratio somewhat dubious and indicates that this character is of subordinate importance.

The form of the rostral crests, also, is not of prime value in estimating generic relationships. The crests develop in the adult from slender-snouted young and are subject to great variation. There are species which show constant differences, but changes seem to have taken place rapidly in the phylogeny and there are some forms such as *Phytosaurus kapffi* and *Machaeroprosopus lithodendrorum* which closely parallel each other in development of the crest.

It might be supposed that the slender-snouted phytosaurs should be separated from the shorter- and heavier-snouted forms and possibly regarded as having preceded them. Yet this can scarcely be. The earliest known form, *Mesorhinus*, is doubtfully restored with a relatively short premaxillary region (Huene, 1911). On the other hand, two of the latest and most specialized species, *Phytosaurus kapffi* and *Machaeroprosopus validus*, have the shortest snouts of any of the well-known forms. Some of the most primitive genera, such as *Angistorhinus* and *Promystriosuchus*, have elongate rostra. We are evidently dealing here with a recently acquired structure subject to very rapid change and consequently relatively useless for our present purposes.

The number of teeth might be taken as an index of specialization. No definite rule can be observed but there seems to be a tendency for the number to be increased in the long-snouted forms. This character is therefore subject to objection on the same grounds as the elongation of the rostrum.

Certain features of the narial region may be susceptible of more definite interpretation. The anterior position of the nares in *Mesorhinus* also appears in the American genera *Promystriosuchus* and *Paleorhinus*, which are certainly primitive in other respects (Case, 1922). The external nares in *Angistorhinus*, *Mystriosuchus*, *Rutiodon*, *Leptosuchus*, *Phytosaurus*, and the young of *Machaeroprosopus* are placed almost directly over the internal nares, with the anterior borders of the external slightly in advance of the internal. In adults of *Machaeroprosopus* the external nares have retreated behind the internal nares. In the European genus *Angistorhinopsis* (Huene, 1922*a*), the nares are farther advanced than in *Angistorhinus* and there are other slight discrepancies in the distribution of this character.

In *Mesorhinus* and *Angistorhinopsis* the nares are of large size and subcircular, in the latter certainly the septum is very thin and the septomaxillaries are small. In *Angistorhinus* and *Promystriosuchus*, the septum is thin and the septomaxillaries are small or absent. In *Paleorhinus*, *Mystriosuchus*, *Phytosaurus*, *Lepto-*

suchus, *Rutiodon*, and *Machaeroprosopus*, on the other hand, the nares are strongly compressed and the septum is thick. Also, in *Leptosuchus*, *Phytosaurus*, and *Machaeroprosopus*, the septomaxillary is large and extensive in front of the nares.

The antorbital vacuity is small and lies behind the anterior border of the nares in the young of *Machaeroprosopus lithodendrorum*. In adults of all species of this genus it extends well in front of the nares, as it does in *Rutiodon* and *Phytosaurus kapffi*. In *Angistorhinopsis* and *Mystriosuchus*, it extends but little anterior to the nares. In *Promystriosuchus*, *Leptosuchus*, *Paleorhinus*, and *Mesorhinus*, it lies entirely behind the anterior border of the nares. This may be significant in connection with the retreat of the nares but it is not always associated with such a condition, *Leptosuchus* being the most striking exception. In this genus the posterior part of the head is very long.

One of the most significant skull characters is the depression of the inner and posterior borders of the supratemporal fenestra. This doubtless accompanies the enlargement of neck and shoulder muscles to serve an increasingly ponderous head.

The primitive state of this fenestra (which originally develops in connection with the temporal muscles) is a dorsal opening in the skull roof bounded in *Paleorhinus* and *Angistorhinus* (and probably also in *Mesorhinus*) by the parietal antero-medially, by the postorbital antero-laterally, and by the squamosal and tabulare behind. In *Promystriosuchus* the posterior parietal process runs back to the posterior border of the opening but is slender. In *Leptosuchus* the posterior process of the parietal is depressed but still meets the squamosal. In all other genera (*Rutiodon*, *Mystriosuchus*, *Phytosaurus*, *Machaeroprosopus*, and *Angistorhinopsis*) the posterior process of the parietal no longer meets the squamosal at the level of the skull roof. This process is much shortened or entirely reduced and the parieto-tabulare is depressed over the posterior margin of the fenestra. This border is higher in *Machaeroprosopus* than it appears to be in *Mystriosuchus plieningeri*. In *Machaeroprosopus validus* the depression of the supratemporal fenestra is carried so far that the opening is scarcely visible from above and the posterior processes of the parietals are lost. In other species of *Machaeroprosopus* which come from lower horizons, in *Mystriosuchus*, in *Phytosaurus*, and in *Angistorhinopsis*, the opening is greatly depressed, though still visible from above and the posterior processes of the parietals are short.

In this respect, therefore, *Machaeroprosopus validus* and *buceros* are the most advanced phytosaurs so far known and the closest relationships are indicated between this genus, *Phytosaurus*, and *Mystriosuchus*.

The posttemporal openings are exceptionally large in *Machaeroprosopus*, even larger and more laterally placed than in *Phytosaurus kapffi*. This region is not well described in *Rutiodon* and may bear similar resemblances in that genus. These openings are also large in *Angistorhinus*.

The squamosal region extends far posteriorly in *Machaeroprosopus* as it also does in *Phytosaurus kapffi* and in *Leptosuchus*. *Mystriosuchus*, *Angistorhinus*, and

Angistorhinopsis show somewhat less of this development, *Paleorhinus* still less, and *Mesorhinus* and *Promystriosuchus* have scarcely anything that might be called a posterior squamosal process.

The relative position and aspect of the orbits vary greatly. In the primitive *Mesorhinus* and *Promystriosuchus* they are very far behind the nares and look upward, the skull being flattened. In *Paleorhinus* and *Angistorhinus* they are turned a little outward. In *Angistorhinopsis* they are very small, set far apart, and look upward and forward more than outward. In *Leptosuchus* they are far behind the nares and look outward as well as upward. In *Belodon*, *Phytosaurus*, *Rutiodon*, and *Machaeroprosopus* they are closer to the nares and look outward more, perhaps, than upward. These characters are associated with elevation (compression) of the skull in later forms and the retreat of the nares.

The character of the palate changes in a very interesting way in the forms represented by the known genera. In *Mesorhinus* there are well developed palatal ridges already present which form an incipient secondary palatal. These ridges however are formed in the posterior half of their extent by the pterygoid bones. In other phytosaurs the margins of the ridges are almost entirely formed by the palatines so that the condition in *Mesorhinus* is apparently not directly related to that in other forms.

In *Promystriosuchus* the palatal vault is entirely open and bordered only by roughened incipient ridges on the palatines. In *Angistorhinus* and *Paleorhinus* and *Leptosuchus*, these ridges are slightly higher, narrowing the vault. In *Mystriosuchus*, *Phytosaurus*, and *Machaeroprosopus* the vault is further enclosed by the ridges of the palatines which overarch below, and were perhaps extended in cartilage to form a soft secondary palate. Here, then, somewhat closer relationships are indicated between *Machaeroprosopus* and these genera than with other forms.

Little can be said of the prevomers because, in most forms, their boundaries have not been carefully worked out.

The transverse in *Machaeroprosopus* and in all other genera except *Mesorhinus*, *Angistorhinus*, *Leptosuchus*, and *Paleorhinus* (?), is extended posteriorly to form a ventrally projecting process which extends below the external wing of the pterygoid. This process is broad and heart-shaped in *Machaeroprosopus*, differing in this detail from *Mystriosuchus*, *Phytosaurus*, and *Angistorhinopsis*. Its enlargement in *Machaeroprosopus* above that of other genera is doubtless concerned with the great weight of the lower jaw and the corresponding size of the internal pterygoid muscles which find their origin on this broadened surface.

The interpterygoid vacuity in *Machaeroprosopus* is somewhat larger and broader than in *Leptosuchus*, *Phytosaurus*, and *Mystriosuchus*. It is at about the same stage of development as in *Angistorhinopsis* and not nearly so large as in *Promystriosuchus*.

Summarizing, we find that in skull characters Machaeroprosopus *is most nearly like the European* Phytosaurus, *and has some closer resemblances to* Mystriosuchus *and possibly to* Rutiodon *than to any other known genera.* Phytosaurus *in its skull appears to be a dwarf form of* Machaeroprosopus.

We are assured by European investigators, however, that the dorsal armature of *Phytosaurus* is made up of quadrangular, flanged plates while that of *Mystriosuchus* consists of subtriangular or irregularly rounded unflanged plates with a roughened median crest, very similar to *Machaeroprosopus*.

I do not find any reference to the effect that the supposed armature of *Phytosaurus kapffi* has ever been found in immediate association with skull elements, so there may still be some doubt as to this conclusion. If it were so, it would surely be sufficient to establish a generic distinction between *Machaeroprosopus* and *Phytosaurus*. It does not necessarily indicate a closer affinity of *Machaeroprosopus* with *Mystriosuchus*, than with *Phytosaurus* or *Rutiodon*. That point must be decided by a study of other parts of the skeleton.

The skeleton of *Rutiodon*, described and figured by McGregor (1906), has been compared with some of the European genera by Huene (1913). The skeletal parts used in making these comparisons were necessarily taken from several individuals, possibly from several different species. In certain cases it is by no means clear that the parts compared actually belong to the genera to which they are referred. This means that any attempts to compare the skeletons of *Machaeroprosopus* with *Phytosaurus* should be regarded as merely tentative. Somewhat more definite statements may be made concerning the relations of *Machaeroprosopus*, *Rutiodon*, *Clepsysaurus*, and the European *Angistorhinopsis*. There is also a specimen of *Mystriosuchus planirostris* which fortunately includes a skull, dorsal dermal scutes, throat shield, anterior vertebræ, shoulder girdle, ribs, and gastralia.

Huene (1913 and 1922*a*) has distinguished some of the skeletal elements of *Mystriosuchus planirostris* from the supposed parts of *Phytosaurus kapffi*. In the region of the pelvis, hind limbs, and dermal scutes, it seems that the assignments Huene makes might be open to at least the possibility of question. The following comparisons however are based upon descriptions of the European specimens as they are allocated by Huene. *With this in mind it may be stated that most of the skeletal elements of* Machaeroprosopus *resemble more closely those of* Mystriosuchus *and* Rutiodon *than those assigned to* Phytosaurus.

THE VERTEBRÆ

The vertebral series of the types of *Machaeroprosopus adamanensis* and *M. zunii* appear to be complete from the axis to the third caudal (pl. 3). In each specimen there are 25 presacral vertebræ including the atlas. In other phytosaurs the number of presacrals has never been accurately known but has been estimated as 26 in *Rutiodon* and 25 in *Mystriosuchus*.

There are seven cervicals, if this term be used to designate those vertebræ, anterior to the pectoral girdle, whose ribs do not reach the sternum. In *Rutiodon* the number of cervicals is estimated to be "7 to 9." In *Mystriosuchus planirostris* it is known to be seven. The beginning of the dorsal series is not marked by the position of the parapophysis but by the greatly increased size of the articular

facet on the face of the diapophysis for the enlarged first dorsal rib, otherwise the cervicals grade very uniformly into the dorsal series.

There are 18 dorsal vertebræ, all but the last two of which have movable ribs. There are two sacrals.

The column in *Machaeroprosopus* is arched much more strongly than it is in reconstructions of related genera. The column is inclined upward in the anterior cervical region, arched upward in the dorsal region, and inclined downward behind the sacrum. These points (pl. 3) have been determined by examination and measurement of the faces of the centra and their attitudes.

The neural spines are higher in the cervical, posterior dorsal, sacral, and anterior caudal regions and lower in the anterior and mid-dorsal series. *Machaeroprosopus* is peculiar in having broader, flatter table-tops on the spines of the anterior dorsal vertebræ than are known in any other phytosaurs. These tables support the dermal armor.

The diapophyses increase in length from the anterior cervical to the mid-dorsal region. They are straight and point downward in the anterior cervical region, slightly upward in the anterior dorsal region, and horizontal in the mid- and posterior-dorsal region. They are carried higher on the sides of the neural arches in the mid-dorsal region than elsewhere.

In *Rutiodon* the diapophyses are directed downward in the cervical region, nearly horizontally in the anterior dorsal, and slightly downward in the mid-dorsal regions. In *Mystriosuchus planirostris* conditions seem to be very similar. Vertebræ referred to *Phytosaurus kapffi* have diapophyses inclined slightly downward in the anterior dorsal region and arched very strongly upward in the mid-dorsal region.

The parapophyses in *Machaeroprosopus* are carried on the centra of the third to the seventh cervicals and the three anterior dorsals. In the fourth dorsal the neurocentral suture cuts through the upper half of the parapophysis. Behind this the parapophyses are carried entirely on the neural arch until the twenty-third vertebra is reached. On the seventeenth to twenty-second vertebræ, the parapophyses extend forward beyond the anterior faces of the centra. In the last two lumbars, the sacrals, and the caudals, the para- and diapophyses are fused into a single transverse process. This is suturally united to the rib which abuts on both the neural arch and the centrum.

In *Rutiodon*, *Mystriosuchus*, and *Phytosaurus*, no vertebræ are known in which the parapophysis extends forward beyond the anterior face of the centrum. Also, in *Rutiodon* the ribs of the last two lumbars articulate with the transverse process in the usual way, and McGregor adds a third vertebra in this region in which the parapophysis is carried wholly or partly on the centrum.

The centra in *Machaeroprosopus* are smaller in the posterior cervical region than anywhere else in the dorsal and sacral regions. They are rounded here and in the posterior lumbar sacral and anterior caudal series. They are strongly compressed in the mid-dorsal series and larger there than elsewhere. The centra are

biconcave except of course the centrum of the atlas. The edges of the faces are rounded.

A single mid-ventral keel is present beneath the whole length of the centrum in all the presacral vertebræ with the exception of the atlas. The first sacral and first caudal vertebræ have no keel. The second sacral and the second and third caudals have two longitudinal keels which at the ventral edge of the posterior face of the third caudal pass into the facets for the chevrons. There are no such facets on the first and second caudals.

The zygapophyses are placed higher on the neural arches of the posterior cervicals than elsewhere on the column. The prezygapophyses here are very long and the facets strongly inclined toward the vertical. The mid-dorsal zygapophyses are smaller, lower on the neural arch, and the facets gradually become more horizontally placed until in the caudal series they are nearly level. The zygapophyses in the caudal and posterior dorsal regions are higher in the neural arch than in the mid-dorsal region.

Description and Comparison of Individual Vertebræ.—The atlas is not complete in any of our specimens. It is entirely missing in the type of *M. zunii*, and is represented in *M. adamanensis* by a part of one neural arch, and in *M. lithodendrorum* by a part of the intercentrum and the right neural arch. Another specimen referred to *M. adamanensis* has a complete atlantal intercentrum.

The intercentrum is almost identical with that described in *Rutiodon* by McGregor. The anterior face is more deeply cupped for the reception of the condyle than the posterior face, which is saddle-shaped for articulation with the odontoid. I cannot find any evidence of rib facets on either the neural arch or the intercentrum of the atlas in any of our specimens.

The neural arch is separated by suture from the intercentrum. The base of the neural arch in *lithodendrorum* is only about three-fourths the length of the end of the intercentrum. In *Rutiodon* it is practically as wide as the intercentrum. The anterior spine is more slender than in *Rutiodon* and the posterior spine is shorter and blunter than in that genus.

The apparent absence of rib facets is the most striking peculiarity of our specimens. If these were present they were very much smaller than in *Rutiodon*. Despite the absence of facets there was evidently a small, single-headed atlantal rib present.

The axis is well preserved in four specimens; the types of *adamanensis*, *lithodendrorum*, *zunii*, and a small specimen, (27025), consisting of several cervical vertebræ referred to *adamanensis* (pl. 4). The specific differences between these specimens have already been indicated. The three parts of the axis-odontoid, intercentrum, and axis proper, are fused along their suture lines in the three larger specimens and entirely separate in the smaller. The anterior face of the axial centrum is set back in its lower half to accommodate the intercentrum and accepts the odontoid on the upper half of what would be its normal anterior face. There is a small, depressed rib facet on the lower part of the lateral surface of the

intercentrum. The ventral surface of the intercentrum is nearly flat with the edges much roughened and curled downward for muscle attachment.

The odontoid is very large and, as McGregor has already described, is entirely excluded from contact with the occipital condyle. Its articulation with the atlas is arranged for unusual flexibility in this joint, thus compensating for a certain amount of stiffness in the rest of the neck. The neural spine of the axis is expanded antero-posteriorly into a triangular plate which flares into a broad, grooved or flattened posterior surface and narrows anteriorly into a roughened ridge. The summit is broadened for attachment of the dorsal cervical ligaments. The spine is higher and more nearly vertical in *Machaeroprosopus* than in *Mystriosuchus planirostris* (Huene 1922*a*), and the postzygapophyses are placed much higher on the neural arch with the facets turned more toward the vertical than in *planirostris*. This indicates perhaps a greater possibility of vertical movement of the head in *Machaeroprosopus* along with a heavier neck.

The axis referred to *Heterodontosuchus* by McGregor (1906) probably belongs to *Machaeroprosopus* for reasons which I have previously indicated. The neural spine is perhaps too broad in the restoration (fig. 13) but the postzygapophyses have been restored as they appear in *Machaeroprosopus*. Specific differences between our specimens and McGregor's are indicated in the position of the diapophyses. These are about opposite the center of the odontoid in our species and are opposite the lower margin of the odontoid in McGregor's.

The resemblances of the atlas-axis complex of *Machaeroprosopus* to *Desmatosuchus* do not seem to be so close as Case suggests on the basis of McGregor's restoration.

A peculiarity of our specimens is the development of a rudimentary "prezygapophysis" opposite each side of the neural canal for the very loose articulation of the posterior projections of the well separated halves of the neural arch of the atlas. A peculiarity of *adamanensis* is the development of a "facet" on the centrum of the axis just below and in front of the diapophysis. It does not seem probable that the tuberculum of the axial rib could have extended into this position but there is that possibility and I have so indicated it on the restoration (pl. 3).

The third cervical vertebra differs from all others in the character of its slender spine (pl. 3). The acute summit of this projects above the top of the spine of the axis and inclines a little forward. Its diapophysis is smaller and narrower than on the succeeding vertebræ and the centrum is slightly smaller than the other cervicals. The posterior ventral border of the centrum is carried much farther ventrally than the anterior face. The peculiar character of this vertebra has not been recognized in previously described material. I am inclined to think that it is more specialized in *Machaeroprosopus* than in other genera.

In comparison with the third, the fourth cervical has a stouter and slightly longer spine and differs abruptly in the expansion of its summit. It is set a little father forward and is also inclined forward. The parapophyses are slightly larger, higher on the centrum, and more extended laterally, while the ventral keel is more pronounced posteriorly.

In the fifth cervical the spine is erect and straight, and longer than in any other vertebra in the column. In comparison with the fourth it is broader and thicker, and more expanded at the summit. The diapophyses are abruptly longer; they are also more deeply cupped than in any of the other cervicals. The neurocentral suture bisects the diapophyses. The parapophyses are slightly larger and project farther forward; the prezygapophyses are larger and higher on the neural arch; they also face inward toward the vertical at a more acute angle; the ventral keel is less pronounced.

The sixth cervical spine is longer than in any other vertebra except the fifth. It is slightly curved posteriorly and is broader, thicker, and more expanded at the summit than the fifth, with a better developed posterior ridge.

Compared with the sixth, the seventh cervical spine is slightly shorter, curved a little more posteriorly, slightly narrower, without as well developed a posterior ridge, and with a more widely expanded summit. The diapophyses are longer and more horizontal. The articular surfaces of the diapophyses are convex rather than cupped, as they are anteriorly. They lie for the first time entirely on the neural arch and are not so depressed as those on the anterior cervicals. The zygapophyses are larger and higher and their faces are more horizontally placed.

Comparison with other described phytosaur skeletons shows that in Machaeroprosopus *the cervical vertebræ are more highly differentiated, with relatively shorter spines and more expanded dorsal tables than in* Rutiodon *and* Mystriosuchus planirostris. *Also the edges of the spines are not so sharply keeled as in* planirostris.

The eighth vertebra (first dorsal), as compared with the seventh has a noticeably shorter spine, which curves posteriorly and is slightly stouter, while the summit is expanded to about the same extent.

The diapophyses are abruptly longer and very much larger. They are furnished, for the first time in the column, with two ventral buttresses and a dorsal, posterior buttress. These buttresses are rudimentary in the seventh. The rib facet on the diapophysis is now large and longer in vertical than in horizontal diameter, the angular ventral corner extending into a ridge which runs beneath the middle of the process. The tip of the diapophysis is for the first time wider than the base. The zygapophyses are larger and higher than on any other vertebra in the column. Their faces are depressed toward the horizontal more than in the seventh, and the parapophyses are larger and placed a little higher on the centrum.

In our material of *Machaeroprosopus* the difference in height of the neural spines of the seventh and eighth vertebræ is more noticeable than in *Rutiodon* and *Mystriosuchus planirostris* but is not so abrupt as in a series of vertebræ referred by Huene (1922*a*) to *Phytosaurus*.

The ninth vertebral spine projects backward farther than the eighth, so that a plane laid across the posterior face of the centrum passes in front of the flanges on the summit of the spine. As in the eighth, the summit is expanded broadly, and the transverse processes are longer and relatively more slender. The dorsal posterior buttress is narrower and the mid-ventral ridge and the concavities at the anterior and posterior sides of the base are deeper. The mid-ventral keel is weak.

The tenth vertebral spine is projected backward as in the ninth, but its summit is more expanded, more horizontal, flatter, and more squarish in outline. The diapophyses have larger cavities at their bases than in the ninth and the rib facets are larger. The mid-ventral ridge on the diapophysis is higher, and the faces of the zygapophyses are larger, than in any other vertebra. The parapophyses are abruptly larger, eliptical, and higher on the centrum than they are in the ninth. The mid-ventral keel on the centrum is weak.

The eleventh vertebra is readily distinguished by the great size and position of its parapophysis, which lies on the neurocentral suture in transition between the position on the anterior and mid-dorsal vertebræ. In comparison with the tenth vertebra the neural spine is lower and more upright; the diapophysis is broader and thicker than in any other vertebra, and more nearly horizontal than in the tenth, but the facet is not quite so large, while the cavities at the base are larger, the faces of the zygapophyses are more nearly horizontal, and the mid-ventral keel on the centrum more pronounced, than in the tenth.

Compared with the eleventh, the twelfth vertebra has a slightly higher spine with a more broadly expanded dorsal table. The diapophyses are slightly longer, more elevated, and more flattened, and the ventral ridge is weaker. The posterior fossa is smaller and the anterior fossa also is much reduced, being encroached upon by the parapophysis. The parapophysis is for the first time entirely upon the neural arch and its rib facet is not more than one-fourth as large. This is no indication of the size of the rib itself, however, which is one of the longest and largest of the series. The zygapophyses are lower, slightly smaller and face more nearly horizontally. The centrum is oval in cross section and the mid-ventral keel sharper.

The thirteenth vertebra is similar to the twelfth except for the less expanded summit of the spine, the somewhat more slender, longer, and higher diapophyses, the smaller and more elevated parapophyses which now join the edge of the diapophysis, and the nearly horizontal facets of the zygapophyses.

The fourteenth vertebra resembles the thirteenth except for the less expanded summit of the spine, the closer union of diapophyses and parapophyses, the more elevated and more anteriorly projecting parapophysis, and the more compressed centrum.

The fifteenth vertebra resembles the fourteenth except for the smaller tables on the summit of the spine, the slightly longer, higher, and more backwardly projecting diapophyses, the closer union of parapophysis and diapophysis, the elevation above the centrum, and the extension forward of the diapophysis.

The sixteenth vertebra is similar to the fifteenth except for its more compressed spine which is less expanded dorsally, its diapophysis with an antero-ventral furrow extending to the tip, its more widely separated dia- and parapophyses, which now for the first time lie nearly in the same plane.

The seventeenth vertebra has the main characters of the sixteenth with slight differences: (1) spine not so greatly expanded at summit, more clearly erect; (2) parapophyses with nearly vertical facets.

The eighteenth vertebra is still less expanded at the summit of the neural spine than the seventeenth, the tables being now reduced to mere swellings. The anterior groove in the spine is replaced by a sharp ridge. The transverse processes are shorter, more slender, and project upward more than in the sixteenth, and the parapophysis projects forward slightly more and laterally a little less than in the sixteenth.

The nineteenth vertebra differs from the eighteenth in the slightly higher, more vertically compressed and longitudinally elongated neural spine, in transverse processes a little shorter and with tips of diapophysis raised higher on the neural arch and projecting upward to a greater degree than in any other vertebra in the column; anterior fossa at base of diapophysis reduced; keel on centrum very weak.

The twentieth vertebra differs from the preceding in its more erect and anteroposteriorly elongate spine, its lower, smaller, shorter, and more flattened diapophysis, and its parapophysis extended forward beyond the prezygapophysis. In *M. zunii* the parapophysis of the nineteenth vertebra also extends beyond the prezygapophysis. The centrum is one of the most compressed of the series.

The twenty-first vertebra differs from the twentieth in its slightly higher spine, less expanded at the summit. Its transverse process is shorter and more depressed, with the anterior and mid-ventral fossa more restricted. The parapophysis extends forward beyond the prezygapophysis. *Zunii* possesses a keel in the centrum, but there is scarcely a trace of one in *adamanensis*.

In comparison with the twenty-first vertebra, the twenty-second has a higher and more erect spine, the diapophysis is shorter and weaker and for the first time lies below the level of the parapophysis which reaches forward just to or beyond the prezygapophysis. There is a trace of a keel on the centrum.

The twenty-third vertebra has a broader spine than any in the column except the axis. The spine is higher than in the twenty-first, and more constricted at the base. There are no traces of flanges on summit. The diapophyses are depressed nearly to the centrum and are much narrower and weaker than in the twenty-first. Zygapophyses are higher than on immediately preceding vertebræ. Parapophyses lie well behind prezygapophyses as well as behind anterior face of centrum and are elevated above diapophyses. Centrum is shorter and wider than in preceding dorsals. There is a trace of a keel.

The twenty-fourth vertebra differs abruptly from the twenty-third in having the para- and diapophyses very short, fused, and *united by suture to the ribs*. The spine is high and narrow for the first time in the dorsal series. The anterior fossa at the base of the transverse process is more extensive than in the posterior dorsals. The posterior fossa is obliterated, the mid-ventral fossa nearly or entirely so. The parapophysis is carried on the centrum in this and the next following vertebra, these being the only ones in the posterior dorsal region in which this happens. The centrum is smaller and more cylindrical than in the twenty-third, the faces of the centrum being circular rather than oval. A keel is present. The ribs of this vertebra are tapering and pointed at their tips.

The twenty-fifth vertebra (last dorsal) is similar to the preceding except that its spine is higher, its transverse process slightly lower. Also the process is slightly shorter and stouter, and its posterior and mid-ventral fossæ are entirely obliterated. The faces of the zygapophyses are more vertically placed than on the other posterior dorsals, where they are nearly flat. This vertebra differs from the twenty-fourth in that the parapophysis extends farther downward on the centrum, and is short, extending laterally a little farther than the prezygapophysis. The centrum is more flattened, the height being less than the width. There is a single median keel.

The posterior face of the centrum is peculiar in having elongate vertical facets developed at each side for articulation with the extended flanges adjacent to the anterior face of the centrum of the first sacral. These facets while not roughened or ankylosed to the succeeding centrum undoubtedly contribute to the rigidity of this joint. They are more highly developed in the species *zunii* than in *adamanensis*. The ribs of this vertebra are flattened at their tips and united by suture to the transverse processes as in *Clepsysaurus*.

The twenty-sixth (first sacral) vertebra has a higher spine than any of the dorsals. The summit is not expanded. The processes are very short and stout supporting the greatly enlarged first sacral rib with which it unites by suture. The anterior base of this rib develops a projecting flange which articulates with a facet on the posterior face of the centrum of the preceding vertebra, as just described. The anterior fossa at the base of the transverse process is smaller than in the twenty-fifth. The zygapophyses also are smaller, and are set in a more nearly vertical plane.

The parapophyseal portion of the transverse process extends nearly to the base of the centrum, and is much larger than the diapophyseal (neural) portion. The centrum is about the same size as in the twenty-fifth, but has traces of a double keel as in the caudal series. The anterior face of the centrum is flattened and the posterior face is firmly ankylosed to the centrum of the second sacral. The zygapophyses, however, continue to articulate in the normal way. The rib of this vertebra is thicker and not nearly so broadened horizontally as in the second sacral. It is fused at the posterior margin of its tip with the anterior margin of the tip of the second sacral rib.

The twenty-seventh (second sacral) vertebra is similar to the first sacral except for the character of the anterior face of its centrum and the great size of its transverse processes which are stouter and broader than in any other vertebra. The anterior fossa is almost obliterated. In comparison with the twenty-sixth, the anterior zygapophyses is very small—little more than half as large. The postzygapophysis is, on the other hand, a third again as large, while the centrum is larger and is weakly double keeled. The second sacral rib is very broad and its tip lies at an angle of about 30° to the horizontal. In specimens referred by Huene (1922*a*, figs. 10*d*, 11*b*) to *Phytosaurus*, this articular face of the second sacral rib is tilted upward at an angle of about 60° to the horizontal, and the extremity

of the first sacral rib is more expanded horizontally than in our material of *Machaeroprosopus*.

The postzygapophysis of the first sacral and the prezygapophysis of the second sacral are smaller in these specimens of *Phytosaurus* (?) than in *Machaeroprosopus*.

In *Rutiodon* the anterior sacral, which McGregor has identified as the second sacral (1906, pl. 10, fig. 40), has a rib which differs decidedly from *Machaeroprosopus* in being broadened in the vertical plane at its tip rather than in the horizontal plane.

In *Rutiodon* and *Phytosaurus* no tendency to ankylosis between the sacrals has been observed. In a specimen of *Angistorhinopsis* figured by Huene (1922*a*), ankylosis has taken place between the last dorsal and the first sacral but this is probably pathological. A sacrum of an adult phytosaur from Crosby County, Texas, described by Case (1922), differs from *Machaeroprosopus* in the much greater distal expansion of the sacral ribs and the apparent lack of ankylosis between the centra as well as in characters of the ilium and ischium.

The twenty-eighth (first caudal) vertebra of *Machaeroprosopus* has a high compressed neural spine without dorsal expansion and similar to the spines of the last dorsal and the sacrals. As in the sacrals the shaft of the spine curves forward slightly. The transverse processes are extremely short and joined by suture to the flattened ribs which are similar to those of the last dorsal vertebra. The anterior fossa at the base of the transverse process is bounded medially by a sharp thin ridge as in the sacrals and the last dorsal. An incipient ridge of this sort is present in the next to the last dorsal as well. The zygapophyses are very large and set at an acute angle to each other. The blades of the zygapophyses extend for the first time far forward beyond the centra. The posterior face of the centrum is at a lower level than the anterior to accommodate a downward curvatuer of the tail, and the anterior face of the centrum is concave along its vertical axis. The centrum is flattened beneath, has traces of a double keel and no chevron facets.

The twenty-ninth (second caudal) vertebra is similar to the twenty-eighth but with somewhat lower postzygapophyses and more pronounced double keel below the centrum.

The thirtieth (third caudal) vertebra is similar to the preceding but with a slightly lower spine, with prezygapophyses projecting farther forward and with small facets for the chevrons developed at the intersection of each ventral keel with the posterior face of the centrum.

In *Phytosaurus kapffi*, vertebræ described by Huene (1922*a*, figs. 14–16) as anterior caudals have much lower spines than in *Machaeroprosopus* and the spines have expanded summits.

In specimens assigned to *Mystriosuchus* the anterior caudal vertebræ have much more elongate, slender spines and smaller ribs than in *Machaeroprosopus*. The summits of the spines are not expanded.

In a specimen from Texas assigned to *Phytosaurus* by Case (1927) but which probably represents an American genus, the neural spines of the two anterior cau-

dals and the sacrals are slightly higher than in *Machaeroprosopus* but otherwise the vertebræ are very similar.

In *Rutiodon* the spines of the anterior caudals are about the same height as in *Machaeroprosopus* and are very slightly expanded at the summit.

To summarize.—The vertebral characters of Machaeroprosopus *are sufficiently distinct from those of other described genera to confirm the separation of this form. The distinguishing characters include the greater curvature of the column, the greater flattening of the summits of the anterior dorsals, the attitude of the diapophyses of the mid-dorsal series, the forward extension of the parapophyses of the posterior dorsals, the reduction of the atlantal ribs, the fusion of the sacral centra, and the characters of the sacral ribs.*

In *Machaeroprosopus* the cervical spines are more differentiated, shorter, and more expanded dorsally than in *Rutiodon* and Belodon *planirostris;* the dorsal spines, anteriorly at least, are shorter than in any other described genera, except *Desmatosuchus.* In the mid-dorsal and caudal series the spines in *Phytosaurus* are shorter and more expanded than in *Machaeroprosopus* and *Rutiodon,* which in turn have shorter caudal spines than *Belodon planirostris,* and *Leptosuchus* ?.

Machaeroprosopus *appears to be more specialized in the cervical region than any other genus of true phytosaurs. In the mid-dorsal, sacral, and caudal regions nearly all the distinctive characters are intermediate between those of* Mystriosuchus *and* Phytosaurus *with somewhat closer resemblances perhaps to the former and to* Rutiodon (cf. pls. 3, 4).

THE SHOULDER GIRDLE

The pectoral girdle (figs. 14, 15) is complete in the type specimen of *M. adamanensis* except for a short mid-section of the interclavicle and the entire left clavicle. The scapula and coracoid in this specimen are firmly united by suture and have been retained in this condition on both sides during petrifaction. In paratype (26717) the separated surfaces show a deeply interdigitating sutural joint which was undoubtedly immobile. In a specimen referred to *Phytosaurus* (Huene 1922*a*) this surface is smooth. In *Rutiodon* and *Mystriosuchus,* it is apparently roughened as in *Machaeroprosopus.* I should consider it an age character were it not for the fact that the type of *adamanensis* is not so large as some of the paratypes.

In general proportions the scapulo-coracoid is closer to Rutiodon *and* Mystriosuchus *than to* Phytosaurus. *The scapula differs from the first-named genera, however, in the development of a broad process overhanging the supracoracoid notch. In this respect it resembles* Phytosaurus *and* Angistorhinopsis.

The acromial portion of the anterior border of the scapula is broadened into a pronounced curvature. The vertebral border is widened and the presence of a cartilaginous suprascapula is indicated in the flat roughened surface over the extent of the vertebral border.

The point of juncture of the clavicular ligament is indicated by a thickened and slightly roughened area of narrowly elliptical outline situated upon a flattened eminence (acromion) on the anterior border of the scapula at the level of the dorsal border of the glenoid.

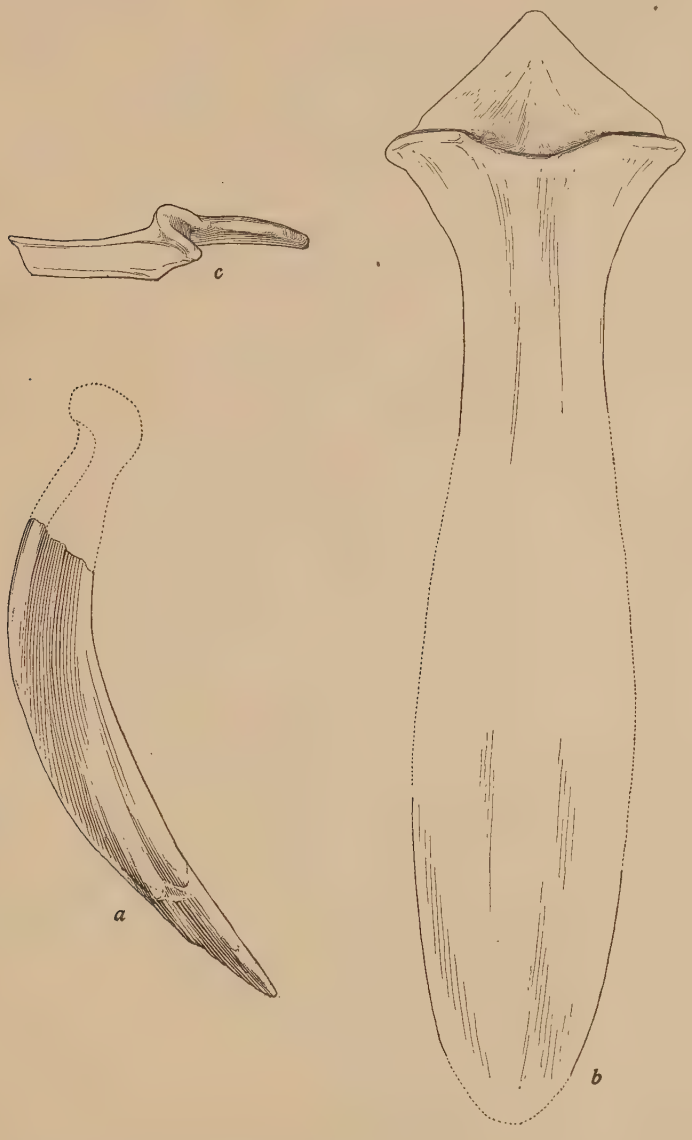


Fig. 14. Clavicle and interclavicle of *M. adamanensis* (type), ×⅓. *a*. Clavicle, right side, posterior view. *b*. Interclavicle, ventral view. *c*. Head of interclavicle, right side.

The origin of the long head of the triceps is indicated by a circular, slightly raised and roughened area about 18 mm. in diameter, the center of which lies about 4 cm. above the dorsal border of the glenoid and about 1 cm. behind the supraglenoid notch.

The subscapular surface is divided into two portions by a low, rounded ridge which runs diagonally from the deepest portion of the edge of the glenoid forward and upward to the middle of the anterior scapular border. Here the ridge encloses one side of a shallow groove provided with a small central ridge doubtless for the attachment of fascia.

This ridge presumably divides the inner face of the scapula into two areas of muscle attachment; a dorso-posterior group comprising the serratus and subscapularis, and an antero-ventral group consisting of the omotrachelius dorsalis and levator scapulæ ventralis of Monotremes.

A point of interest is that we have the beginning of a supraspinous fossa comparable with that of *Cynognathus* (Gregory and Camp, 1918, pl. 40). Such a development in this phytosaur is doubtless due to the great size and mobility of the head.

The coracoid is undivided and contains no foramen. It differs from *Rutiodon* in the development of a deep subglenoid notch, the presence of a broad posterior border, and a larger supracoracoid emargination. In the first two of these characters it resembles the specimen figured by von Meyer (1865, pl. 27, fig. 10) which is referred by Huene to *Phytosaurus*. In proportion of length to breadth, however, it bears a closer resemblance to *Mystriosuchus*. The broadening of the posterior border distinguishes it from hitherto described forms. This border was doubtless in extended articulation with a cartilaginous sternum.

The median border of the coracoid is furnished with a flat, slightly roughened surface for the attachment of an epicoracoidal cartilage. The dorsal surface of the plate is deeply excavated for the reception of the subcoracoideus muscle. Bounding this excavation anteriorly is a rounded buttress which forms the posterior border of the supracoracoid notch.

The clavicle (fig. 14) has a more symmetrical crest than in previously described material. It lacks a small part of the medial end but the shape of this as reflected in the fossæ of the interclavicle was evidently a hook-like knob. The acromial end is extended to a sharp point not quite reached by the thin, curved, ventral border. The posterior border is flat medially and shows faint traces of two terminal grooves at the acromial end, which are so distinct on *Rutiodon*. The anterior border is flat, slightly hollowed dorsally.

The clavicle resembles those described for Angistorhinopsis *and* Rutiodon *more closely than that described for* Mystriosuchus.

The interclavicle (fig. 14) has the general shape of a similar element (*Machaeroprosopus?*) from Tanner Crossing, Arizona, figured by Huene (1926, fig. 3). It differs slightly in the shape of the clavicular fossæ—these being excavated more deeply toward the mid-line in *adamanensis*—and in the greater size of the head. *Resemblances to* Mystriosuchus planirostris *and to* Rutiodon carolinensis *are closer than to the specimen referred to* Phytosaurus kapffi (Huene, 1922*a*, fig. 27).

There is a mid-ventral ridge anteriorly and two longitudinal ridges on the dorsal surface of the posterior half of the blade.

THE PELVIC GIRDLE

This girdle (fig. 15) is nearly complete in the types of *M. adamanensis* and *M. zunii* and there is some other pelvic material of the former species, including the pelvis accompanying skull and skeleton 27008. Certain differences between

Fig. 15. Scapulo-coracoid of *M. adamanensis*, ×⅓. Right side, median or inner side.

these specimens which are considered to be specific or sexual have already been indicated. The task of comparing our material with that of other genera is attended with much uncertainty owing to the fact that only in *Rutiodon* and *Angistorhinopsis* is this material associated with skulls.

A synopsis of the differences and resemblances between the various ilia so far described in the literature and our own material will be found in table 5.

Table 5 shows that closest resemblances are seen between our material of *Machaeroprosopus* and an ilium from Holbrook, Arizona, figured by Mehl. Mehl assigns this specimen to *Angistorhinus* in his plate caption but in his description he suggests that the specimen belongs to *Machaeroprosopus*. The latter is evidently the case. I should, however, hesitate to assign the specimen to any known species of the genus.

Very close resemblances appear in the ilium assigned by Sinclair to *Rutiodon manhattanensis* and now tentatively placed in the genus *Clepsysaurus*.

Close resemblances are also shown to an ilium from Texas described by Case (1927); the complete girdle of this specimen is known and differs from our species of *Machaeroprosopus* in the nearly vertical position of the pubis, and in the greater height of the neural spines of the anterior caudal and the sacral vertebræ. There are certainly closer resemblances to *Machaeroprosopus* than to *Phytosaurus*, and I suggest that the specimen be tentatively assigned to the former. There is more than a possibility that it belongs to the species described by Case as "*Phytosaurus*" (=*Machaeroprosopus?*) *doughtyi*.

Some close similarities are shown to a specimen (*Mystriosuchus* ?) described and figured by von Meyer (1865, pl. 29, fig. 1). But in our specimens the total length is greater, the pubic sutural surface is broader, and the acetabulum does not show a division into two parts. None of the ilia referred to *Mystriosuchus* show any marked differences from *Machaeroprosopus*.

In respect to the ilium, Machaeroprosopus *is less similar to* Rutiodon *than to* Mystriosuchus. *In* Rutiodon, *the ilium is not so high, while the muscular tubercle above the acetabulum on the crest is more pronounced than in* Machaeroprosopus *and* Mystriosuchus.

Case's material from Texas, with the exception of the University of Michigan number, 7244, previously mentioned, is not closely related to *Machaeroprosopus*. In fact the differences are much greater than those between our material and *Rutiodon* and *Mystriosuchus*. It might be suggested that his specimens may belong to *Promystriosuchus* (7470, 7322) and *Leptosuchus* (7266, 7333). This assignment would be based upon the enlarged lateral tubercle present on the iliac crest in the two latter forms and the elongate pre-iliac process in the two former.[5]

In view of the resemblances between skulls of *Machaeroprosopus* and *Phytosaurus*, it is unusual to find such great differences between the ilia of these two genera. The most obvious differences are of course the great elongation and depression which this element has undergone in *Phytosaurus*, the acuteness of the post-iliac process and the hypertrophy of the supra-acetabular buttress and flattened process on the iliac crest.

[5] See also Case, *Mem. Univ. Mich. Mus.*, vol. 2, 1929, p. 51.

TABLE 5

RESEMBLANCES AND DIFFERENCES BETWEEN SPECIMENS OF PHYTOSAUR ILIA

Characters in circles are so different from our species of *Machaeroprosopus* as to practically exclude close relationship to that genus.

Characters in squares are closely similar to our species of *Machaeroprosopus*.

Association of many of the specimens with the genera given here is questionable.

		Machaeroprosopus, U. C. Coll., 4 specimens	*Machaeroprosopus* sp.? Mehl, 1916, pl. 2	"*Phytosaurus*" *doughtyi*?, Univ. Mich. 7244, Case, 1922, fig. 27c and pl. 13b; and Case, 1927.	*Clepsysaurus manhattanensis*, Sinclair, 1918, fig. 5.	*Promystriosuchus*?, Univ. Mich. 7470, Case, 1922, fig. 27b.	*Promystriosuchus*?, Univ. Mich. 7322, Case, 1922, fig. 28b.	*Leptosuchus*?, Univ. Mich. 7266, Case, 1922, fig. 27e.	*Leptosuchus*?, Univ. Mich. 7333, Case, 1922, fig. 27d.	*Rutiodon carolinensis*, McGregor, 1906, pl. 10.	*Belodon*?, von Meyer, 1865, pl. 29, fig. 1.	*Belodon*?, von Meyer, 1861, pl. 41, fig. 3.	*Belodon*?, von Meyer, 1861, pl. 41, fig. 4.	*Belodon*? *juv.*?, von Meyer, 1861, pl. 41, fig. 5.	*Belodon*?, Huene, 1922*a*, fig. 30.	*Phytosaurus*?, von Meyer, 1861, pl. 41, fig. 1.	*Angistorhinopsis*, Huene, 1922*a*, fig. 106*a*.
1. Muscular process on anterior portion of crest	Absent			×								×	×	×	×		×
	Small	×	×		×	×	×			×	[×]						
	Enlarged							(×)	×							(×)	
2. Relation of length to height of acetabulum	Less											×					
	Equal					×					×		×		×		
	Greater	×	×	×	×		×	×	×	×				×		(×)	×
3. Relation of length of post-iliac process to length of crest anterior to post-iliac notch	Less					(×)	(×)		×					×	×		×
	Equal									×	×		?				
	Greater	×	×	[×]	×			×				×				×?	
4. Relation of length across ischio-pubic border to total height	Less					×											
	Nearly equal	×	×	×	×						×	×	×	×	×		×
	Greater						×	×	×?	×						×	
5. Relation of juncture of ischio-pubic border to pre-iliac notch	Anterior			×								×	×				
	Below	×	×		×	×	×										
	Posterior							×	×?	×	×			×	×	×	×
6. Relation of pubic articular surface to ischial	Shorter				×	×	×			×		×	×	×	×		
	Equal	×	×								×					×	×
	Longer			×				×	×?								
7. Relation of length of pre-iliac process to length of pubic border	Less than half	×	×	×	×					×	×	×	×	×			
	About half																×?
	More than half					(×)	(×)	×	×						×	(×)	
8. Outline of crest just behind pre-iliac process	Straight												×		×		×
	Bowed upward	×	[×]	×	×	×	×	×	×	×	[×]	×		×		×	
9. Outline of ischial suture	Bowed inward	×		×	[×]						[×]	×?			×	×?	×
	Straight							×	?	×							
	Bowed outward		×			×	×						×	×			
10. Total length divided by greatest height	*zunii*	1.73															
	adamanensis 1	1.63	1.54	2.16	1.62	1.46		2.14		1.90	2.14	1.77		1.93	1.58		
	adamanensis 2	1.79															
11. Greatest height divided by length across pubo-ischial suture	*zunii*	.99															
	adamanensis 1	.95	.91	1.00	.80	1.12	.94	.86		.80	1.04	.97	1.00	.92	1.00	.72	.98
	adamanensis 2	89															

The ilium which Lees (1907, fig. 8) has assigned to *Paleorhinus* is distinct from all others now known. The elongate acetabulum and enormous supra-acetabular process seem to bring it closer to *Phytosaurus* than to *Machaeroprosopus*. The same features give it some resemblances to the ilium (of *Leptosuchus*) figured by Case (1922, fig. 27*e*).

The pubis is complete on the right side in the type of *M. adamanensis* and on both sides in the type of *zunii*. The differences between these specimens are very slight. In the former the obturator foramen is round, in the latter it is smaller and elliptical. In the former there is a notch cut into the antero-lateral process, in the latter this process is smoothly rounded.

The resemblances to a specimen described by Case (1927) are closer than to any other genera available for comparison. As previously indicated I should be inclined to give this specimen a place within the genus *Machaeroprosopus*.

These specimens of ours, *Clepsysaurus manhattanensis*, and, apparently, the specimen described by Case (1927), are distinctive in the great expansion of the pubic plate. This is accompanied by an enormous increase in the area of the pubo-iliac sutural surface, this surface being at least twice as long as in the specimen figured by von Meyer (1865, pl. 27, fig. 11). The dilation of the pubic plate has given the pubis a quadrilateral outline in *Machaeroprosopus* and *Clepsysaurus* instead of the triangular or rounded outline seen in *Rutiodon*, *Mystriosuchus*, and *Phytosaurus*.

This expansion of the pubis is doubtless correlated with an increased development of limb musculature in connection with terrestrial life. The great size of the puboischiofemoralis muscles is also indicated by the deeply roughened areas to which they attach on either side of the enlarged fourth trochanter of the femur. These muscles support the hind quarters in walking.

Other differences between our specimens and previously described forms are: lateral border of pubis more evenly curved; an abrupt angle between anterior border and symphysis; anterior border not advanced beyond the antero-lateral process as it is in *Rutiodon;* total length equal to (*zunii*) or slightly less than (*adamanensis*) the length of the iliac crest. The character of the anterior border of the pubic plate indicates that this surface was continued in cartilage.

An interesting condition in the character of the pubis is the variation seen in the "drop," or relation of the plane, of the pubic plate to the vertical in the various species and genera. The "angle of drop" as used here is the angle between a plane drawn to include the three most anterior points of the pubis and a horizontal plane drawn through the iliac crest. This angle is about 35–40° in *Rutiodon*, 50° in *M. zunii*, 55° in *M. adamanensis*, 60° in *Belodon?* (Huene, 1922*a*, fig. 30), 62° in *Angistorhinus*, and 70° in the specimen from Texas described by Case (1927). Some of these differences might be explained on the assumption that in females the depressed lower border of the pubis accommodates an increased size of the body cavity. But I am not inclined to regard the extreme differences as sexual.

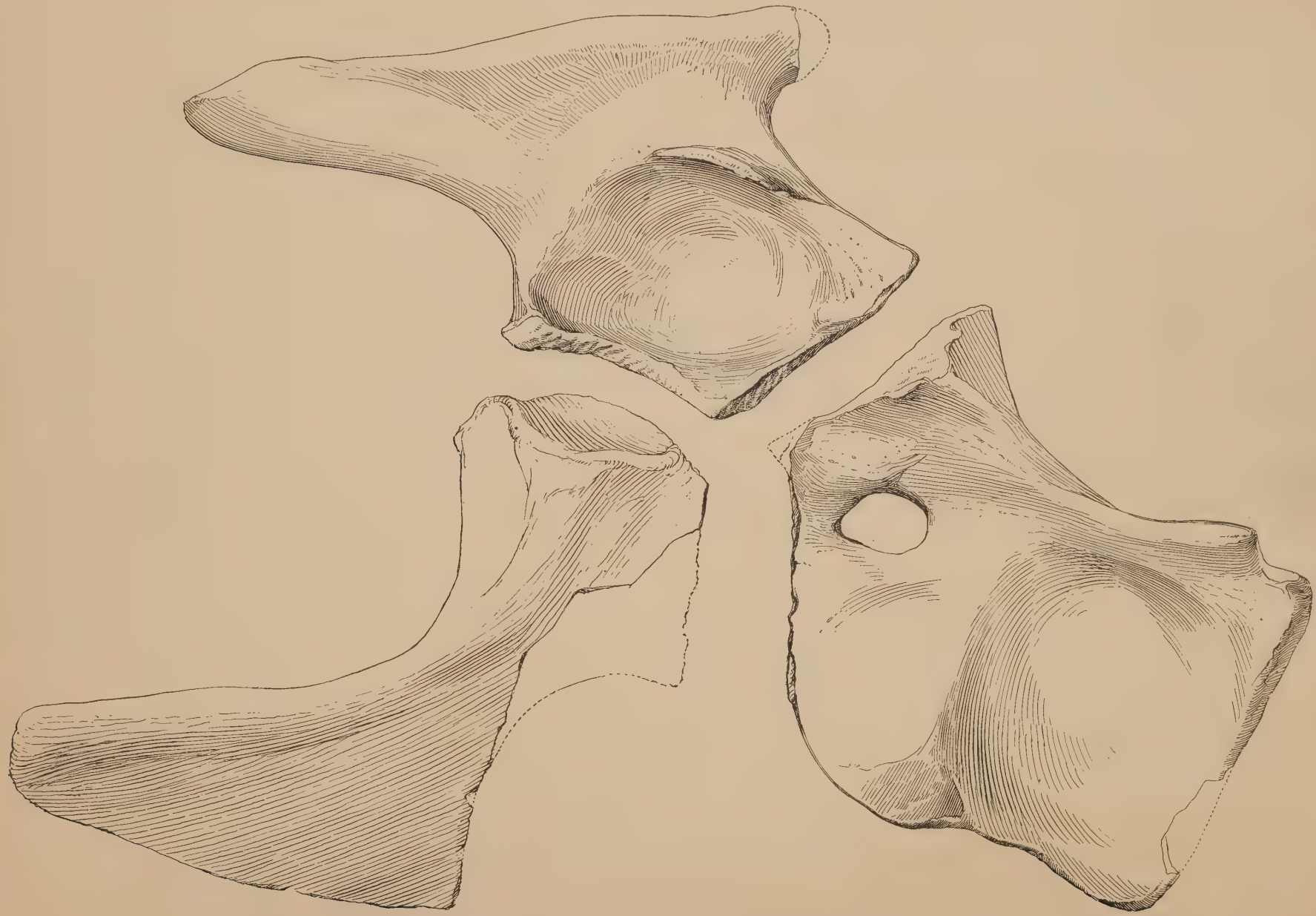


Fig. 16. Pelvis of *M. adamanensis* (type), ×½. Right side, lateral view.

The ischium is nearly complete on the left side in the types of *M. zunii* and *M. adamanensis*, and in another specimen of the latter (27008, U. C. Mus. Pal.,). The type of *M. zunii* (fig. 7) differs from all previously described phytosaurs in having a deep, semicircular notch on the pubic border of the ischium. This means that the ischio-pubic fenestra was almost entirely surrounded by bone. It is likely that in all phytosaurs this fenestra was completely closed below by the symphyseal cartilage. There is a slight emargination in the ischial border of the pubic to accommodate the anterior margin of the fenestra. The bone at the periphery of the fenestra is very thin, making it appear that the presence of the fenestra is due to the thinning of the ischial blade under the action of the obturator muscles, which must have been of increased size in these forms. This may in turn be correlated with increased terrestrial activity.

In specimens of *adamanensis* the pubic border of the ischium is partly broken away but it is likely that a fenestra similar to that of *zunii* was present. There is, however, in *adamanensis* no corresponding notch in the ischial border of the pubis, which is roughened for the attachment of a thin cartilaginous border.

In *adamanensis* the symphyseal borders of the ischium are beveled in such a way as to make it apparent that the bone extended to the mid-ventral line. In *zunii*, however, this is not the case and there may have been a broad symphyseal cartilage. This may be a sex difference.

The caudal border of the ischium is straighter than in Mystriosuchus *and* Rutiodon. *The total length of the element is 230 mm. in the type of* adamanensis, *this being relative to other features, about the same as in* Mystriosuchus *and* Rutiodon *and much greater than in* Phytosaurus.

THE FORE LIMB

Two complete humeri are at hand (fig. 17, nos. 26757, 26717) both from the Blue Forest, lower level, in exactly the same horizon and within a few hundred feet of the type of *M. adamanensis*. Each is from the right side. They are of nearly the same size and show nearly identical characteristics.

The width of the head of the humerus enters the total length between two and one-half and three times. In *Mystriosuchus* and *Phytosaurus kapffi* this width enters the length two and one-half times or less. In *Rutiodon* the width of the head is contained in the length considerably more than three times. In a humerus described by Huene (1920, fig. 1) from the upper Muschelkalk of Bayreuth, the width of the head is contained over four times in the length. The humeri of *Angistorhinopsis* are not complete. The left humerus of this form as restored by Huene (1922*a*, p. 136) has a head width entering the total length about two and one-half times, or slightly less, but this ratio is not certain. The humerus from Bristol, referred to *Rileya platyodon* (Huene, 1911, p. 44, figs. 31–35), is very slender medially but the incomplete head is broad, being anterior in the total length from two and one-half to three times. The shape differs considerably from *Machaeroprosopus*.

The only humerus previously described which might be assigned to *Machaeroprosopus* is one in the United States National Museum collections from near Tanner Crossing, Arizona (Huene, 1926, fig. 4). In this specimen the width of the head enters the total length slightly more than two and one-half times.

In *Mystriosuchus*, *Phytosaurus*, and *Angistorhinopsis* the length of the deltoid crest is less, in *Rutiodon* it is much greater, than the head width. In our specimens of *Machaeroprosopus* it is equal to the head width.

Fig. 17. Humeri of *M. adamanensis*, right humeri, median side, ×¼. *a*. 7038/26717. *b*. 7038/27094.

In *Mystriosuchus*, *Phytosaurus*, and *Rutiodon* the median portion of the head is not so small and high as in *Machaeroprosopus*. In this respect *Angistorhinus* is closer than other described forms.

The internal condyle is more highly developed in *Machaeroprosopus* than in other described genera and apparently the olecranal fossa is more extensive than in other described genera except *Rutiodon*, where it is equally large.

The entepicondylar groove is less developed than in the European forms perhaps more so than in *Rutiodon*.

To summarize.—The humerus of Machaeroprosopus *is more slender than in the European forms but not so slender as in* Rutiodon. The *articular surfaces are more highly developed than in other known forms. The deltoid crest is more elongate than*

in the European forms. These are further indications that Machaeroprosopus *was a more active animal on land than were* Mystriosuchus, Phytosaurus, *and* Rutiodon.

The ulna in our collections is represented only by a right proximal portion of an individual of *M. zunii* (27053) and a left distal portion from the vicinity of Adamana possibly belonging to *M. lithodendrorum*. The olecranon is shorter than in *Rutiodon* and the glenoid appears to be broader than in that genus with a longer lip on its anterior edge. The olecranon is longer, however, than in No. 7312, University of Michigan, figured by Case (1922, fig. 29*e*). The proximal, posterior border of the shaft was also straighter than in Case's specimen.

The distal extremity is very thick and rounded with an anterior rounded condyle as in *Rutiodon*, but flatter on the terminal articular surface than in that genus. The glenoid surface at the proximal end is more deeply excavated apparently than in other phytosaurs described in the literature, with the possible exception of *Episcoposaurus* (Huene, 1915, fig. 27) from which the present specimens differ in their stouter proportions and thicker shafts.

A peculiarity is the development of a deep trough on the median side of the proximal part of the shaft. This is something like that seen in *Rutiodon* but is placed farther caudad and runs nearly to the tip of the olecranon. It doubtless accommodated some of the long flexor muscles of the foot, more powerfully developed as walking muscles in *Machaeroprosopus*.

The radius is represented by only three specimens; a proximal extremity belonging with the ulna of *M. zunii*, just described; another fragment of the same specimen which I regard with some hesitation as the distal extremity; and still another from near Adamana, which may be the same.

The head of the radius is broadened and resembles in this respect the specimen figured by Case (1922, fig. 29*d*). It is closer to this specimen than to either *Rutiodon* or *Mystriosuchus*. The shaft is slender and much narrower than the head. The distal extremity is broader than the shaft, and the articular surface is globular and considerably visible in side view.

THE HIND LIMB

One femur in our collection is complete (*M. gregorii*, 27200). Three specimens referable to *M. adamanensis* (26725, 27008, and 26718) are nearly complete (fig. 18). All are from the left side. Nos. 26725 and 26718 are from the lower Blue Forest beds in the same horizon as the type of *M. adamanensis* and within one-half a mile of that specimen. No. 27008 accompanies a skull and portions of a skeleton from the uppermost Blue Forest beds, one mile south of the type locality of *M. adamanensis*. No. 27200 was found thirty feet from the type skull of *M. gregorii* and may belong with it. Besides these, there is the head of an enormous femur from the lower St. John horizon (fig. 18) possibly referable to *M. zunii*, and a number of other fragmentary specimens.

The femur of Machaeroprosopus *is long, slender, and nearly straight, resembling* Rutiodon *and* Clepsysaurus *in these respects.* The shaft is heavier and more expanded proximally than in *Rutiodon,* also the head is wider in respect to the length, and the condyles and trochanters more fully developed. The width of the head enters the total length three and three-fourths times; in *Rutiodon* it is contained seven and one-half times in the total length. The fourth trochanter is exceptionally long and ends posteriorly in a roughened boss. It is lower than in

Fig. 18. Femora of *Machaeroprosopus,* ×¼. *a. M. adamanensis,* 7038/26718; left femur, ventral view. *b. M. zunii,* 7307/27156; left femur, dorsal view.

a specimen (*Machaeroprosopus* ?) from Tanner Crossing, Arizona (Huene, 1926, fig. 2). It has a sinuous border bounding distally and anteriorly the distinct area of insertion of the puboischiofemoralis externus muscle. This area is very roughened in 26718 and 27200 and is a deeply excavated pocket in 27008. Terrestrial habits are indicated. The femur of *M. adamanensis* differs from that described as *Typothorax* (Huene, 1915, figs. 1, 2) in the lesser development of the condyles. The fourth trochanter is more elongate than in *Typothorax,* though not quite so high.

It seems that the fourth trochanter of *adamanensis* is developed distally for the accommodation of the puboischiofemoralis posterior as well as for the femoral tendon of the coccygeofemoralis on its proximal portion.

The great extent and development of the fourth trochanter separates these femora of Machaeroprosopus *from others previously described. The great width of the head and the curvature of the narrow posterior articular surface of the head are characteristic of this genus and of* Clepsysaurus (cf. Huene, 1913, figs. 11, 12; 1922*a*, figs. 48, 49; Sinclair, 1918, fig. 4; and Case, 1922, fig. 29*b*).

Age characters appear in the two very large specimens, 26718 and 27156. In the former, which probably represents an animal larger than the type of *gregorii*, there is a "fifth" trochanter on the antero-dorsal portion of the shaft at the insertion point of the iliofemoralis muscle. This muscle possibly develops a tendon at its terminus in contrast to the fleshy condition in the American alligator.

No. 27156 is a gigantic femur with a condyle width of 165 mm. in contrast to the width of 125 mm. in *grėgorii*, and 130 mm. in 26718, indicating an animal of enormous size. There is a large, rounded boss for attachment of a circular tendon on the flat, dorsal surface of the head (fig. 18). This was for the insertion of the quadratus lumborum.

All the above femora develop a very distinct, roughened surface for the insertion of the puboischiofemoralis internus muscle anterior to the fourth trochanter.

There is some indication that the puboischiofemoralis externus arose from two heads or was divided into two parts. A roughened area 40 mm. proximal to the fourth trochanter is separated from the normal insertion point of this muscle by a smooth area. Otherwise, these muscle areas on the femur point to conditions very similar to those seen in the alligator.

The visible muscle insertions on the femur indicate considerable development of certain body and tail muscles used in swimming, as well as great strength and enlargement of muscles used to support the hind quarters in walking.

As developed in dinosaurs the fourth trochanter does not necessarily imply swimming habits but is developed in connection with the great size and weight of the tail. In phytosaurs the development of a strong quadratus lumborum, in addition to a stout caudi-femoral musculature indicates a powerful swimming mechanism along with walking adaptations. The latter are in advance of anything to be seen in other phytosaurs except *Clepsysaurus*, which appears to be a very similar form.

Pits and scratches made before petrifaction appear upon femur 26718, U. C. Mus. Pal. These are distributed in a semicircle of four or five deep broken pits about 20 mm. apart on the side of the internal condyle, continued in scratches and grooves spaced the same distance apart (20 mm.) upon the greater trochanter and on the anterior force of the shaft on its anterior border in the curvature just beneath the head (fig. 18). It seems plausible that these marks were made by the teeth of some carnivore that fed upon the flesh and bones of this phytosaur.

As in the case of the femur, the tibia is a longer and more slender bone than in the European phytosaurs. It appears to be even more slender than in *Rutiodon,* but the only two complete tibia in our collections are from a rather young animal (fig. 19; 27008) and may not be so stout as in the adult.

The shaft is somewhat bowed away from the fibula and slightly bowed outward as well. The articular surfaces are both concave, but their thin edges are usually broken away leaving convex surfaces as figured by Huene and McGregor.

The cnemial crest is flattened and a slight notch is present under the fibular side of the head, perhaps for the accommodation of the fibula, perhaps a muscle attachment. A large roughened and slightly excavated area is present on the expanded fibular surface of the shaft just beneath the head. A small raised roughened area is developed on the anterior margin of the shaft in its proximal third. Along the broadened distal third of the anterior margin of the shaft is a shallow groove. On the median side of the distal third of the shaft is an extensive fossa. A mid-section of the shaft is roughly triangular. The two ends are flattened laterally.

The tibia of Machaeroprosopus *is more slender than in any of the previously described forms, the greatest width of the head enters the total length about three and one-half times. In* Rutiodon *it is contained about three times, and in* Phytosaurus *about two and one-half times, in the total length.*

The proximal two-thirds of the right fibula is preserved in the type of *M. zunii.* The distal end is represented by a specimen from near Blue Forest (27014). This represents the right fibula of a very large animal. There is a large iliofibularis trochanter on the middle of the outer surface of the shaft, seen also in *Belodon, Mystriosuchus,* and *Phytosaurus* (cf. Huene, 1922*a*, figs. 53, 54).

In addition there are two other trochanters on the middle of the shaft, one on the anterior border at the level of the iliofibularis trochanter, the other on the posterior border just below the trochanter. There is a fourth trochanter on the antero-median border of the shaft just below the head of the fibula. The head of the fibula is more like that ascribed to *Mystriosuchus* than to *Phytosaurus.* It differs from *Mystriosuchus* in having the articular surface placed at a greater angle to the axis of the shaft.

The distal extremity of the fibula, as in *Mystriosuchus,* has a median ridge on its external surface. This ridge bounds posteriorly a pocket.

The articular surface of the distal extremity is set at an angle to the shaft as in *Mystriosuchus,* but is considerably broader than in *Mystriosuchus* when viewed end on. The median surface of the shaft at its distal extremity is roughened across its whole extent.

The great development of the trochanters, if not due in part to breakage, is an additional indication of great strength of the limb and foot musculature, and may be a further expression of the terrestrial adaptations of *Machaeroprosopus.*

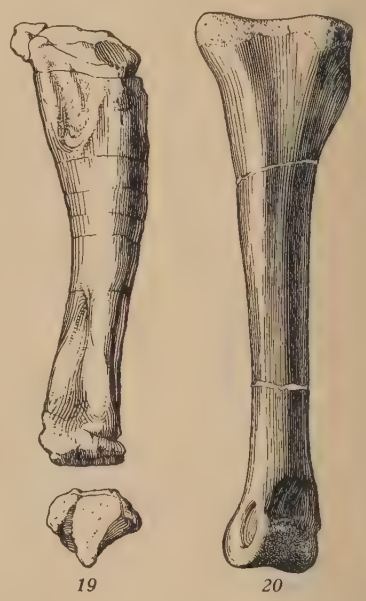
FOOT BONES

A single tarsal element, a tibiale (fig. 19), was found in place at the distal end of the left tibia of a skeleton assigned to *M. adamanensis* (27008). This astragalus differs considerably from the specimen figured as an astragalus by Huene (1926, fig. 6, *a*, *b*, *c*). It is likely that Huene's specimen is some other element.

Tibiale 27008 is about the size and shape of a pullet's egg, but is flattened dorso-ventrally and has a strong median posterior process. The upper (tibial) articulation is rounded, the lower (tarsal) articulations are rounded on the external side and concave on the inturned side. The fibular (external) end is larger than the median end and slightly thicker. There is a short groove on the anterior surface.

No other tarsal elements can be identified with certainty.

One complete metacarpal (fig. 20) is at hand. It is apparently the third from the left foot. While found within a few feet of the type skeleton of *M. zunii*, it probably does not belong with this specimen because of its small size.



19 20

Fig. 19. Right tibia and tibiale of *M. adamanensis*, 7040/27008, posterior view, ×¼.

Fig. 20. Third (?) left metacarpal of *M. zunii*, associated with, but probably not belonging to, 7307/27036, ×1.

The proximal end is much broader than in a specimen of *Mystriosuchus planirostris* figured by Huene (1922*a*, fig. 44). The shaft is more slender than in *Alligator*. The distal condyle differs from *Alligator* in having deep oval pits on each lateral face.

A fragment of the proximal end of a right metacarpal (?) element is present in the type skeleton of *M. zunii*. It is very large and the dorsal tubercle is well developed. The shaft is much flattened and probably was slender.

Two distal phalangeal elements are at hand from the Blue Forest. Since reptiles other than phytosaurs are rare in these beds, I take these to be phytosaurian. They are much stouter than the European specimens figured by Huene (1922*a*, figs. 65, 66) and resemble *Rutiodon* (McGregor, 1906, fig. 29) in this respect. The condyles appear to be better developed than in *Rutiodon* and the distal muscular processes in one of our specimens are very pronounced.

Indications are that Machaeroprosopus *was a shorter-footed form than* Mystriosuchus, *which offers further evidence that the former was a more terrestrial animal.*

THE RIBS

The true ribs are well represented in the types of *M. zunii* and *M. adamanensis*, also in specimen 27008 of the latter. As illustrated (fig. 21), there is a very small, short, flattened rib which doubtless belonged on the atlantal intercentrum. This rib has no tuberculum and is very much shorter than in *Mystriosuchus planirostris*. The axial rib may be wrongly restored on plate 3. It is represented only by a fragment. It may be more like the supposedly atlantal rib figured by McGregor (1906, fig. 30).

The anterior thoracic ribs (pl. 3) are abruptly longer than the cervicals and are provided with a pronounced anterior spine. The anterior dorsal ribs are not so greatly flattened on the exterior (lateral) surface and not so much bowed as those farther back. They are subcircular, distally and subtriangular proximally, in cross-section.

The posterior thoracic ribs are elliptical distally and semicircular proximally in cross-section, with the flattened surface on the outer side.

The posterior dorsal ribs are slender and cylindrical; *the two posterior ones are fused to the transverse processes and the last is much flattened. In* Rutiodon *the two posterior ribs are free. In* Clepsysaurus, *which may not be generically separable from* Machaeroprosopus, *the posterior rib is fused, flattened, and reverted to articulate with the tip of the first sacral rib.*

The tips of the dorsal ribs (except the two posterior ones) are broadened and flattened to accommodate strong cartilaginous extensions which may have been of considerable length.

GASTRALIA

Abdominal ribs (=parasternalia or gastralia) are represented in our collections by a few perfect segments and fragmentary parts associated with the type skeletons of *M. zunii* and *adamanensis*. There is also material from the latter species (27008).

As in *Mystriosuchus planirostris*, the abdominal ribs are in three sections, a central ⋀ chevron element and one lateral splint on each side. The median elements appear to be flattened and broadened at the angle more than in *planirostris* (cf. Huene, 1922*a*, pp. 83–84) and the angle is not less than 90°, whereas in *planirostris* it is sometimes less. The median sections are grooved posteriorly to accommodate the thin anterior edges of the lateral splints. Some of them show traces of a median anterior process.

The lateral splints are not so uniformly curved as in *planirostris* but are usually curved abruptly at one point which doubtless corresponds to the ventro-lateral line of the body. *Evidently* Machaeroprosopus *was abruptly flattened across the belly while* Mystriosuchus planirostris, *presumably a more thoroughly aquatic form, was rounded along the lower parts of the sides.*

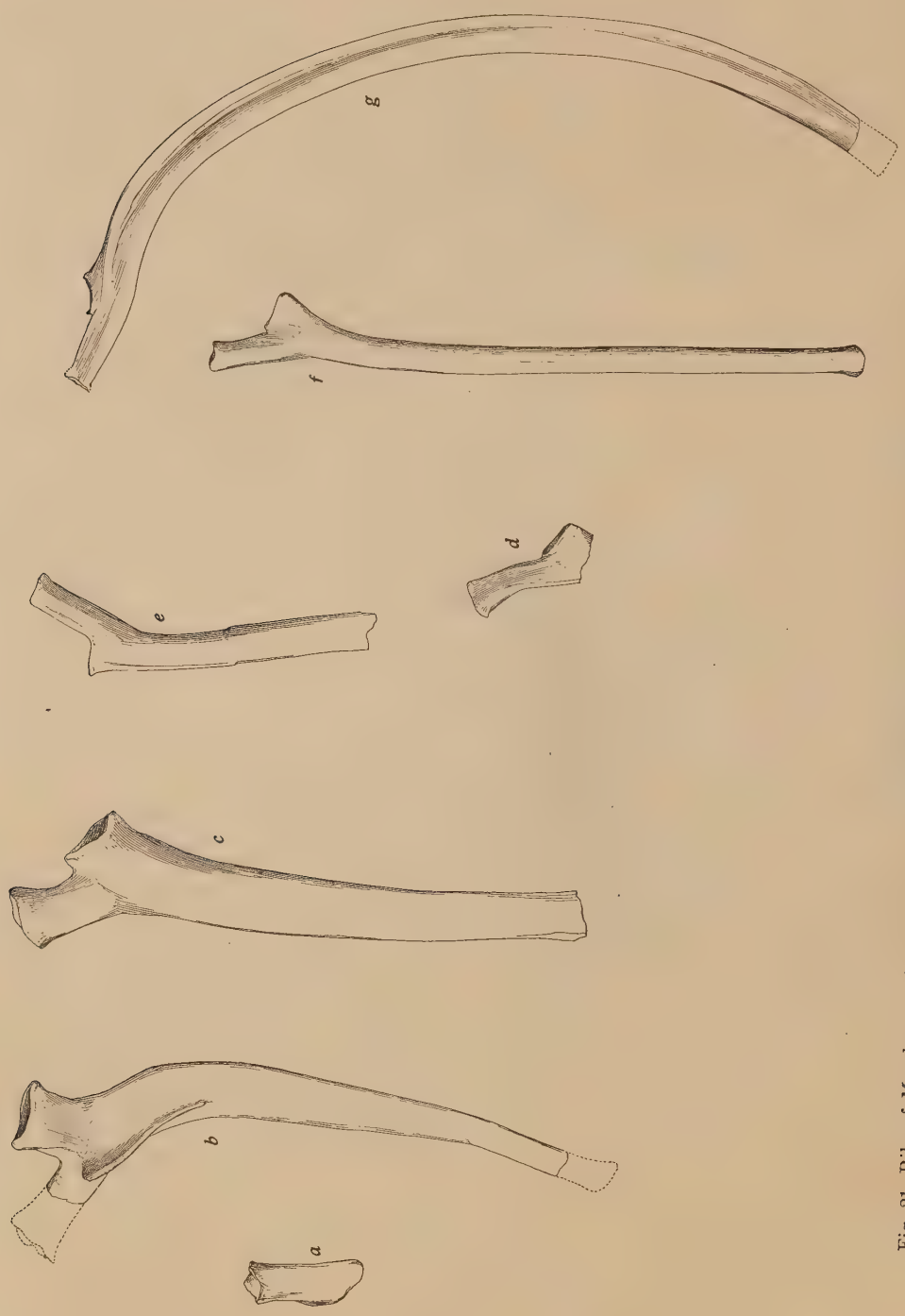


Fig. 21. Ribs of *M. adamanensis*, ×⅓. Figs. *a–f* are of 7038/26699. *a*. First cervical (=atlantal) rib, right side, outer view. *b*. Eighth (=first thoracic) rib, left side, outer view. *c*. Fifteenth (=eighth thoracic) rib, left side outer view. *d*. Head of twenty-first rib, left side, outer view. *e*. Head of twenty-second rib, right side, outer view. *f*. Twenty-third (=last free dorsal) rib, left side, outer view. *g*. A left mid-dorsal rib of 7040/27008, anterior view; to show what is thought to be the natural curvature.

DERMAL SCUTES

Dorsal dermal scutes are preserved in most of the specimens of which we have skull material. I do not attempt to determine specific differences in these scutes but those of *M. zunii* appear to be somewhat more squarish in outline than the others. The skeleton of the type of *M. adamanensis* rested upon a layer of nine pairs of mid-dorsal scutes preserved in nearly their natural position and resting under the spines of the fifteenth to the twenty-third vertebræ. The restoration (pl. 3) is made from these scutes and others found with the same specimen; the positions of those in the anterior region being more or less doubtful. From this evidence it is certain that the scutes were segmentally arranged, a single mid-dorsal pair to each vertebra. It is also certain that each plate overlapped its successor by about one-third of its length. The lateral scutes were subcircular, much smaller than the median, with thin edges all around, and with a central comb. They were apparently intercalated between the tips of median scutes. There was apparently only one lateral row on each side of the body and some additional very small scutes on the sides of the neck.

The median pairs are thickened along the mid-line and they articulate loosely by suture. The combs on the posterior, mid-dorsal series are set at an angle to each other while those farther forward are more widely separated and more nearly parallel. Over the shoulder the combs are low and blunt.

The dorsal dermal scutes of Machaeroprosopus *do not differ appreciably from those of* Rutiodon *and* Clepsysaurus. *They are not so deeply sculptured nor so nearly quadrangular as in* Mystriosuchus *and* Angistorhinopsis. *There may be a more definite mid-dorsal suture in* Machaeroprosopus *than in the other genera mentioned.*

I am still skeptical as to the association of the peculiar scutes described as belonging to *Phytosaurus kapffi* and the known skull material of that form. A few scutes of this "phytosaurus" type have been found in the Chinle Triassic. One specimen from St. Johns occurs in the same horizon and the same vicinity as *M. zunii* and consists of fifty or more of these rectangular and quadrangular scutes, all doubtless from the same individual. Skull fragments in association are phytosauroid, a stouter, broader-headed form than *Machaeroprosopus*, but apparently with an elongate snout.

I do not recall any notice of ventral armature in American phytosaurs with the possible exception of some scutes figured by Cope (1893, pl. 1, figs. 9, 10) in his description of *"Belodon superciliosus."* A ventral breastplate of small interlocking scutes is known in the European genera *Mystriosuchus* and *Angistorhinopsis*. It has not been described in *Rutiodon* and has not been found in association with *Machaeroprosopus* or *Clepsysaurus*. However, in a small lot of fragments collected by the Alexander expedition in 1921, in the vicinity of Adamana,

but from an unknown horizon, there are sixteen of these breast scutes. In the tray with them is the tip of a phytosaur squamosal which is unlike that of any described species of *Machaeroprosopus*. It seems likely that another genus of phytosaur is represented by these fragments.

The plates are of irregular shape with jagged edges and are all less than 7 cm. in diameter. They are from 5 to 7 mm. in thickness and are set with small holes on the ventral (exterior) surface. They are not so deeply sculptured as in *Mystriosuchus* being more like those of *Angistorhinopsis* in this respect (cf. Huene, 1922*a*, p. 139).

SUMMARY

The following characters appear to be more highly expressed in some species of *Machaeroprosopus* than in any other known phytosaurs:

1. Posterior position of the nares (all species).
2. Depression of the supratemporal fenestræ (*validus* and *buceros*, less so in *andersoni* and *tenuis;* other species similar to *Phytosaurus*, *Mystriosuchus*, *Rutiodon*, *Leptosuchus*, and *Angistorhinopsis* in this respect).
3. Extreme differentiation of the posterior premaxillary teeth (*gregorii*).
4. Increase in number of the enlarged anterior premaxillary teeth (3 in validus).
5. Development of the secondary palate (most pronounced in *andersoni*).
6. Elongation of the internal choanæ.
7. Reduction of the palato-transverse (post-palatine) fenestræ (especially in *andersoni*).
8. Broadening of the posterior portion of the transverse.
9. Differentiation of the vertebræ, ankylosis of the lumbar ribs and sacrum, and elongation of the tibia.
10. Increase in size of the fourth trochanter of the femur.
11. Great size of the skull and trunk.
12. Increase in attachments of muscles for terrestrial locomotion.

The following characters are shared by *Machaeroprosopus*, *Mystriosuchus*, and *Rutiodon*, and differ from what is known of *Phytosaurus:*

1. Nasals far forward, well beyond nares (also in *Leptosuchus*, *Angistorhinus*, *Angistorhinopsis*, and *Paleorhinus*).
2. Anterior end of antorbital vacuity beyond nares.
3. Dermal scutes subtriangular and rounded, irregular in outline, usually with medial crest and without smooth, raised anterior flange.
4. Form of femur, dorsal vertebræ, spines of anterior caudals, shape of interclavicle and ilium resemble corresponding structures of *Mystriosuchus* and *Rutiodon* more closely than *Phytosaurus*.

The following skull characters are shared by *Machaeroprosopus* and *Phytosaurus:*

1. Rostrum in some species elevated into a crest. Prenarial portion in some species short.
2. Posterior process of squamosals elongate, equal in length or longer than diameter of eye (also in *Leptosuchus*).
3. Posttemporal opening equal to foramen magnum in size (also in *Angistorhinus*).
4. Dentition highly differentiated (also in *Leptosuchus*).
5. Septomaxillary elongated anteriorly (also in *Leptosuchus*).

The following skull characters are shared by *Machaeroprosopus*, *Phytosaurus*, *Leptosuchus*, *Mystriosuchus*, and *Rutiodon:*

1. External nares elongate, compressed (also in *Paleorhinus*).
2. Narial septum thick.
3. Posterior borders of supratemporal fenestræ depressed (also in *Angistorhinopsis*).
4. Posterior processes of parietals short at level of skull roof, depressed posteriorly (also in *Angistorhinopsis*).
5. Post-choanal vault of the palate narrowed by inward growth of medial palatal ridges (incipient secondary palate), also in *Angistorhinopsis.*
6. Transverse underlaps external process of pterygoid (also in *Paleorhinus*, *Promystriosuchus*, and *Angistorhinopsis*).
7. Parasphenoid rostrum long (also in *Angistorhinus*, *Promystriosuchus*, and *Angistorhinopsis*).

The following characters formerly considered of generic value (Case, 1922) are highly variable in *Machaeroprosopus:*

1. Elevation of narial rim (sex character).
2. Number of teeth.
3. The pre-postnarial ratio.

The following characters are so doubtful in many genera as to have little or no systematic value at present:

1. The palatal extent of the prevomers.
2. The extent of the tabular portion of the parieto-tabulare, behind the supratemporal fenestra.

MORPHOLOGICAL DESCRIPTIONS

Skull Structure of Machaeroprosopus

The form and relations of most of the superficial skull elements of several genera of phytosaurs are for the most part well known and do not require extended notice here. Points which need study are the relations of the palatal bones, the elements constituting the brain case, the olfactory and auditory regions, the narial and choanal septa, the cranial foramina, the posterior aspect of the skull and the problem of independent motility of the quadrate, pterygoid, and basicranial sections.

We are fortunately in possession of a perfect skull, the type of *Machaeroprosopus gregorii*, which it is possible to examine with precision. In preparing this skull, record has been kept of all sections traversed by critical sutures, including several complete horizontal sections through the cranial walls. In one of these sections the cavity of the inner ear is well shown, also the brain cavity.

The following descriptions of cranial structures are based upon this specimen (A 272/27200, U. C. Mus. Pal.), and a number of other skulls and dissociated skull elements (particularly 7037/26699, 7037/27070, 7307/27159, and A 270/27195). These permit a satisfactory understanding of the exact boundaries of the skull elements, the nature of the sutures, and the courses of the foramina.

BONES OF THE SKULL

The *premaxillaries* are the largest and heaviest elements of the skull, forming the greater portion of the extended rostrum. Each side carries two, sometimes three, enlarged teeth at its extremity, and comprises a little more than half of the alveolar border of the upper jaw. Dorsally the posterior processes interdigitate with the nasals and septomaxillaries (fig. 22). On the palate of *M. adamanensis* (type), the thin points of the palatal processes, underlapping the prevomers, nearly reach the choanæ. In *M. gregorii* (type), the points of the palatal processes extend about 2 cm. along the ventral border of the septum and outline the internal margins of the choanæ for that distance (fig. 25). The premaxillaries and septomaxillaries at their union form the roof of an extensive chamber for the anterior part of the anterior pterygoid muscles (fig. 23). They also meet the turbinal plates at the anterior limits of the olfactory chamber.

The *maxillaries* are joined by serrate sutures to the premaxillaries, nasals, jugals, palatines, ectopterygoids, and prevomers. The palatal sutures between premaxillaries and maxillaries are serrate anteriorly, straight, flat posteriorly, and obliquely intersect the anterior palatal ridges (fig. 24). The maxillaries meet on the palatal mid-line above the premaxillaries and anterior to the tips of the pre-

vomers. Just in front of the choanæ they are slightly separated and each is hollowed ventrally into a cup which receives the prechoanal portions of the prevomers.

The *septomaxillaries* are larger in *Machaeroprosopus* than in other phytosaurs, extending forward along the dorsal mid-line and comprising nearly the whole of the internarial septum (7038/26699, 7307/27159, and A270/27195). They spread out posteriorly on the ventral surface of the nasals (fig. 26). They are unsymmetrical in some specimens owing to tumor pockets which sometimes form in the

Fig. 22. *Machaeroprosopus adamanensis*, type skull, details and sections. *a–b*, ×⅓, *c–f*, ×⅔. *a*. Narial-prenarial region, dorsal view. *b*. Same, ventral view. *c*. Section across *e–f* (figs. *a* and *b*). *d*. Section across *g–h*. *e*. Section across *i–j*. *f*. Section across *k–l*.

anterior borders of the nares (cf. fig. 22, *M. adamanensis* type). Ventrally they carry ridges adjacent to the nares, which doubtless supported the median and posterior walls of the short, vertical, narial sac. In a number of specimens (presumably the females) the internarial portion of the septomaxillary is elevated into a sharp, dorsal ridge.

The *nasals* extend forward considerably beyond the antorbital fenestræ, and enter the dorsal borders of these openings for a very short distance between the maxillaries and lacrimals. Laterally these bones are quite thin, posteriorly they are thicker and form the postnarial hump. In about half of the known specimens, the nasals are elevated into narrow rims around the nares, which is presumably

a female character. The nasals form only about one-third of the dorsal border of the septum (A270/27195) and are cut off sharply below by the septomaxillaries so that their rôle in the formation of the septum is insignificant (fig. 26). Anteriorly they extend forward as narrow processes along the walls of the antorbital muscle chamber and the olfactory chamber. Here they are partly covered by the turbinals or lateral ethmoids (figs. 22, 27).

The *frontals* are elongate and narrow, meeting all the surrounding elements by serrate sutures, except the laterosphenoids (="orbitosphenoids"), which lie against ridges on their ventral surface (figs. 26, 28). They are deeply excavated along the ventral mid-line to receive the extensive olfactory tract and bulbs. Division of the olfactory channel by a ridge indicates a separation of each bulbus into two divisions.

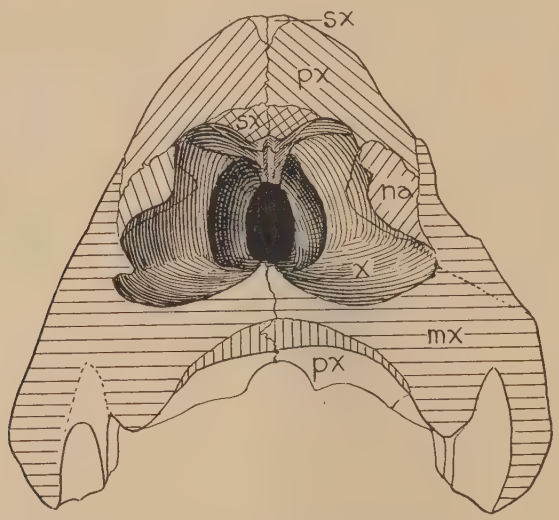


Fig. 23. *Machaeroprosopus gregorii* (type), A270/27200. Section through rostrum, eight inches anterior to nares, showing cavities for insertion of pterygoideus anterior muscles at *x*. Posterior aspect, ×½.

The *parietals* are small, thicker anteriorly, where they meet the frontals, and with a dome-like excavation in the pineal region, just posterior to the center of the combined bones (fig. 25). *Here a pineal pit reaches down from the exterior nearly penetrating the skull* in a young specimen (27181). The foramen is entirely obliterated in all larger skulls. The parietals articulate with the supraoccipital ventrally at the posterior end of the circumference of the inner cranial wall and externally at the posterior end of the median suture. They receive the rounded mid-dorsal tip of the supraoccipital in a small pocket (7307/27159). Antero-ventrally each articulates with the postero-dorsal process of the laterosphenoid. Postero-ventrally and ventro-laterally they are largely fused with the tabulars as described below. Just behind the frontal suture the parietals send down a vertical mid-ventral ridge which meets the olfactory lobes and separates a pair of cavities which communicate posteriorly with the epiphyseal and cerebral regions.

The *lacrimals* lie between the orbits and the antorbital fenestræ. They are bounded anteriorly by the prefrontals and nasals and posteriorly by the jugals and postorbitals, uniting with all by serrate sutures. The lacrimal canal enters at the inner margin of the orbital rim very near the prefrontal suture and passes forward and slightly downward for about 10 mm. where it divides. The lower fork communicates with the spongy interior of the bone in the vicinity of the jugal suture and possibly enters the jugal. The upper fork, about 20 mm. in length, emerges on the inner surface through a foramen which lies about 10 mm. above the dorsal margin of the antorbital fenestra and about halfway to the anterior tip of the lacrimal (fig. 11). The canal lies close to the inner surface, being separated from the interior only by a thin film of bone (7307/27159).

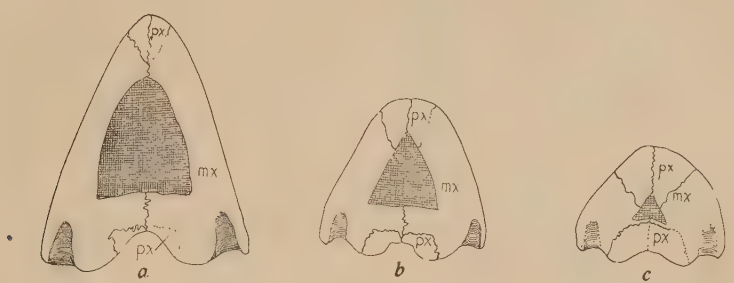


Fig. 24. Sections through rostrum of the type skull of *M. tenuis*, 7043/27018, showing central cavity and relations of maxillaries and premaxillaries, ×½. See fig. 4 for side view of this skull. *a*. Section three inches anterior to nares. *b*. Section five inches anterior to nares. *c*. Section six and one-half inches anterior to nares.

The jugal wing of the lacrimal is excavated on its inner surface into a circular fossa. The jugal wing is separated from the antorbital wing on the inner surface by a sharp ridge running obliquely downward and forward from the orbital opening of the lacrimal canal to the posterior border of the antorbital fenestra. This ridge is a continuation of the raised inner orbital border of the prefrontal. It contributes to the formation of a shelf projecting from the inner side of the posterior angle of the antorbital fenestra (fig. 26).

The *prefrontals* are thick, subtriangular elements elevated into a low ridge in front of the orbits and separated by serrate sutures from the frontals, nasals, and lacrimals which they adjoin. The downwardly projecting, postero-internal tips of the prefrontals barely meet the anterior extremities of the elongate laterosphenoids (fig. 26).

Scrutiny of a number of skulls as they came from the matrix has failed to reveal the presence of bony *sclerotic plates*.

The *postfrontals* are the smallest elements in the skull roof. They are subcircular and adjoin the postorbitals, parietals, and frontals. Ventrally, just within the orbital margins, they are hollowed for reception of the postero-lateral processes of the laterosphenoids. There is a smooth suture at this union; all the others are strongly serrate.

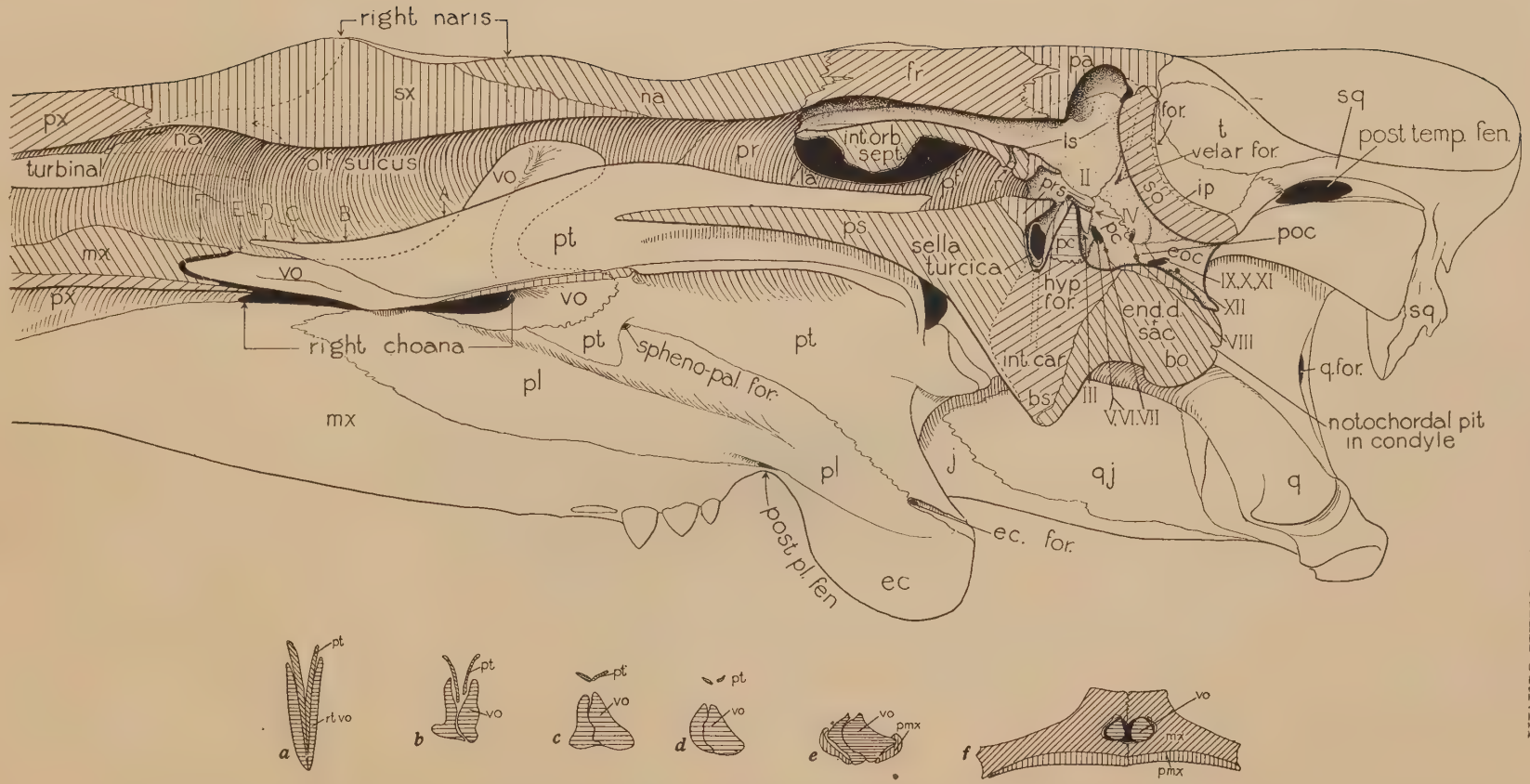


Fig. 25. Sagittal section of skull of *Machaeroprosopus gregorii* (type), A270/27200, ×⅓. Brain cavity dotted. *r*=foramen from olfactory lobes to interorbital region. *end. d*=foramen for endolymphatic duct. *a–f*. location of transverse sections through choanal septum, ×½. *vo*=prevomer. *ip*=interparietal.

The *postorbitals* form the anterior half of each postorbital bar and extend around the posterior and postero-ventral margins of the orbits. A narrow antero-lateral process joins the jugal, and strong sutural unions are formed with this element and with the postfrontals, the parietals, and the squamosals. Ventrally the parieto-postorbital suture extends from the pit for the postero-lateral wing of the laterosphenoid, directly posteriorly, to the anterior margin of the supra-temporal fenestra.

The *jugals* take no part in the ventral margins of the orbits (fig. 9). They form the anterior and ventral borders of the lateral temporal fenestræ and a small part of the postero-ventral margin of the antorbital fenestræ. Each element consists of a dorsal process which joins the lacrimal and the postorbital, an anterior

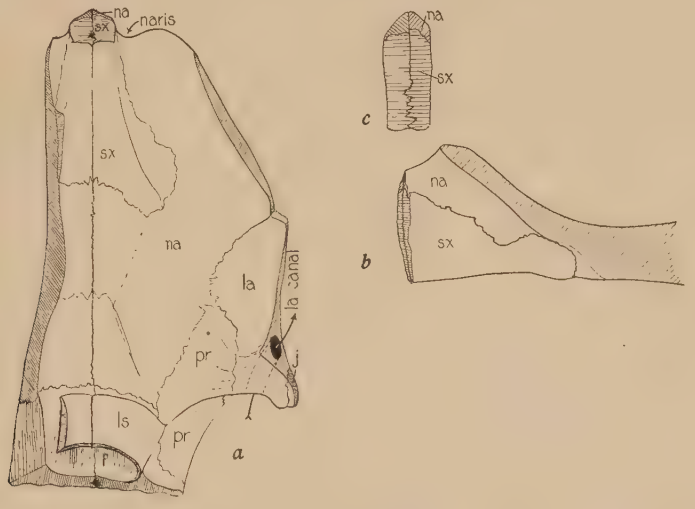


Fig. 26. *M. adamanensis* (type), details and sections of postnarial region, ×½. *a*. Roof of skull between nasals and orbits, ventral view. *ls*=laterosphenoid. *b*. Posterior border of left naris, lateral view. *c*. Transverse section through anterior end of *b*.

portion which articulates with the maxillary, and a posterior process which enters as a wedge between two sheets of the quadratojugal and nearly reaches the quadrate at the level of its condyle. The dorsal process sends down a strong internal ridge which is united by serrate sutures to the dorsal extremity of the ectopterygoid. Anterior to this ridge is a deep pocket.

The *tabulars*.—Under the name "epiotics" Huene (1911, fig. 7) has described and figured elements in *Mystriosuchus* which lie beneath the posterior processes of the parietals. In *Machaeroprosopus* these elements have a different aspect (*cf.* fig. 29). They are elongate bones riding upon the lateral arms of the supra-occipital and extending posteriorly above the supraoccipital bar of the squamosal. Anteriorly they nearly reach the mid-line in the fossa at the dorsal tip of the supraoccipital. From this point postero-laterally for a little more than half their length they are capped by the slender posterior processes of the parietals. Each element has the form of an inverted trough which covers the arms of the supra-

occipital and squamosal and extends downward farther on the median side than the lateral. The sutural unions with the squamosals are smooth. Those with the parietals, laterosphenoids, and supraoccipital are roughened.

Since these bones do not border the inner wall of the brain cavity nor the otic capsules, they must be regarded as part of the primitive skull roof. Their squamosal union and their failure to meet on the mid-line prevent them from being interpreted as the interparietals. Their extensive area on the posterior face of the skull and their failure to establish contact with the postorbitals (from which they are separated by the ventro-lateral parts of the parietals) seems to prevent their consideration as the supratemporals. I therefore regard them as the tabulars.

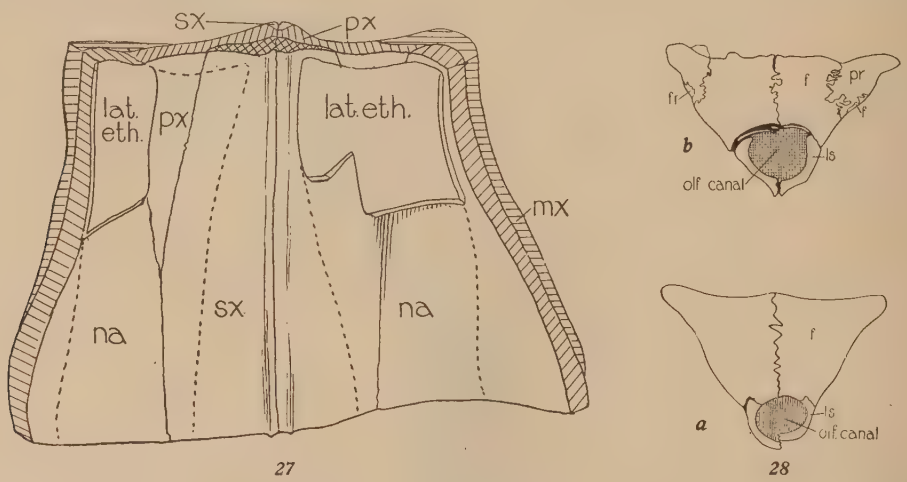


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Fig. 27. *M. gregorii* (type). Roof of skull 3–8 inches anterior to nares, ventral view, ×½. To show location of ossified lateral ethmoids or turbinal plates. Dotted lines indicate portions of the thin lateral ethmoid plates which are broken away.

Fig. 28. *M. adamanensis* (type), transverse sections through frontals between orbits, ×½. *a*. Section through center of interorbital region. *b*. One and one-half inches anterior to *a*.

The tabulars are usually found fused with the parietals in adult skulls. The shape of the combined elements, the symmetry of a pair of dissociated parietals (7307/27070), the occasional presence of parieto-tabular sutures (7307/27159, A272/27200), and the appearance of the line of fusion in cross-sections (A270/27195) is evidence that the tabular has not been lost and occasionally maintains its entire identity.

The *interparietals* (= dermoccipitals) are fused together into an extensive median plate covering nearly all of the posterior face of the supraoccipital, and occupying the position of the vestigial "dermoccipital" of the crocodile as figured and described by Miall and by Mook. Superficially there is usually a faint sculpture shown upon these elements as if the surface were lightly gouged by a small chisel. There is also a pair of variable nutrient foramina near the center of the combined elements.

I have found sutures between these elements and the supraoccipital in only two skulls at hand, (7307/27159, A272/27200, fig. 29). In all other specimens the interparietal plate is indistinguishably fused with the supraoccipital.

The *squamosals* (figs. 3, 30) are quinquepartite. Each sends forward a process to meet the postorbital across the middle of the postorbital bar. An antero-ventral process passes over the upper end of the quadrate and along the anterior rim of the quadratojugal nearly to the postero-ventral angle of the lateral temporal fenestra. This process extends as a broad sheet over the internal surface of the upper end of the quadratojugal and joins the edge of the quadrate above the quadrate foramen. A third process, the paroccipital or "hook-like" process of the squamosal, projects ventrally behind the otic notch and furnishes a smooth surface of articulation for the expanded tip of the paroccipital bone. It does not enclose the auditory meatus as in *Paleorhinus*. It is roughened on the posterior surface for the attachment of powerful neck muscles. The fourth process proceeds forward

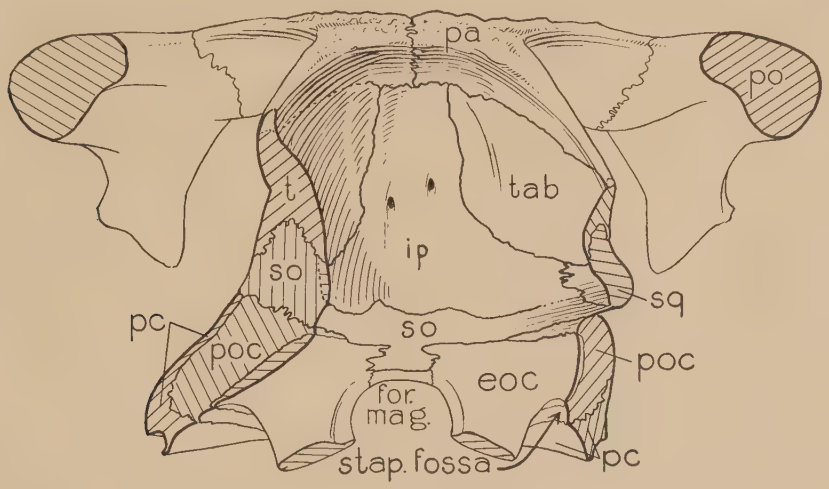


Fig. 29. *M. gregorii* (type), part of posterior aspect of skull showing relations of tabulare (*tab*), interparietal (*ip*) and other elements, ×½.

and medially from the inner face of the squamosal to join the supraoccipital and tabulare above and medial to the posttemporal fenestra. A fifth process, which is a ventral subdivision of the fourth, lies beneath the posttemporal fenestra and is inserted as a thin supporting wedge between the quadrate and the anterior face of the paroccipital. Leaving the paroccipital, beneath the posttemporal fenestra, this process becomes a thin blade which accompanies the dorsal wing of the quadrate to meet the thin quadrate wing of the pterygoid. It overlaps this for a few millimeters at a point directly below the anterior margin of the supratemporal fenestra (fig. 30).

The squamosal receives the dorsal extremity of the quadrate in a deep conical pit just above the otic notch. This pit is smooth on its anterior face but develops a few serrations laterally and posteriorly (7307/27048). For this and other reasons to be enumerated I do not believe that this joint is a movable one, although it doubtless was so in more primitive genera.

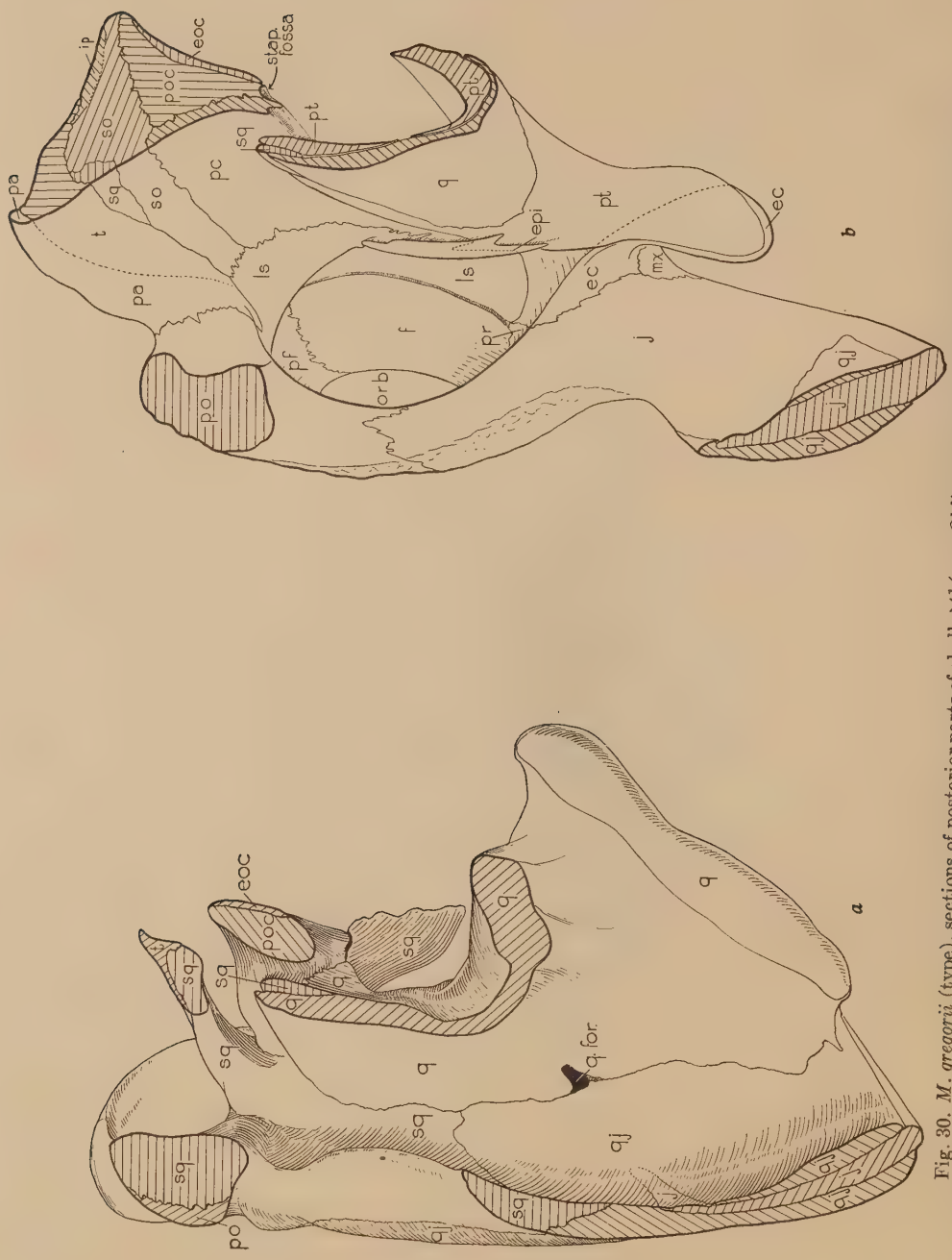


Fig. 30. *M. gregorii* (type), sections of posterior parts of skull, ×½. *a*. Oblique section through posttemporal fenestra and posterior part of quadratojugal bar; right side, antero-median aspect. *b*. Oblique section through middle of postorbital bar, middle of quadratojugal bar, quadrate wing of left pterygoid and middle of left paroccipital; postero-median aspect.

The *quadratojugals* (fig. 30) are extensive triangular plates. The lower portion of each is split to receive the jugal in the way Case (1920) has described in *Machaeroprosopus doughtyi*. The anterior margin does not receive the squamosal in this way but overlaps the squamosal on the outer side extending dorsally to a point above the otic notch. On the posterior face of the skull the quadrate suture passes through the lateral border of the quadrate foramen.

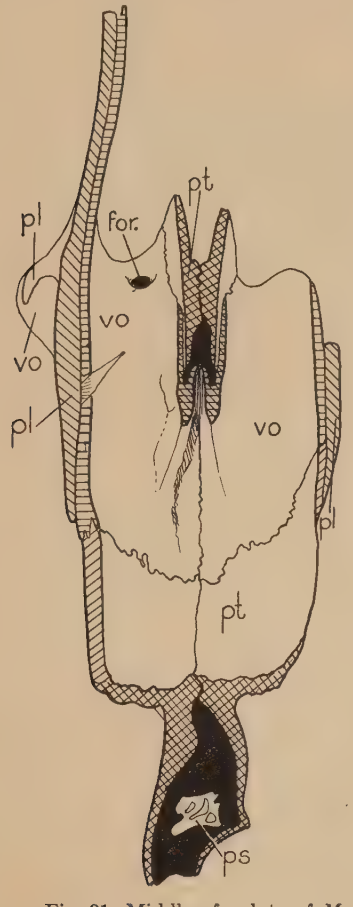


Fig. 31. Middle of palate of *M. adamanensis* (type), showing relations of post-choanal portions of the prevomers (*vo*). Frontal section of lateral borders of palatines and vomers. Transverse section of parasphenoid and pterygoids posteriorly, and oblique section of pterygoids and prevomers anteriorly, ventral view, ×1.

The *quadrates* (fig. 30) are enormous and have complicated relations to surrounding elements. Anteriorly and laterally they join the quadratojugals and squamosals by roughened sutures. The stout dorsal horn of each terminates in a smooth, glazed condyle which occupies a pit in the ventral surface of the squamosal. The pterygoid wing extends forward from this pit and gains contact by means of serrate sutures with the lower lateral surface of the paroccipital (=opisthotic). In this region the quadrate forms a broad trough, the outer end of the stapedial groove. The pterygoid wing, passing forward with a portion of the squamosal, extends over the lateral surface of the quadrate plate of the pterygoid and reaches a point near the base of the epipterygoid as Huene has figured it (1911, fig. 7). This wing of the quadrate extends ventrally as a broad plate and wraps itself around the ventral surface of the quadrate bar of the pterygoid supporting this bar on a broad shelf. The surfaces between quadrate and pterygoid are all smooth and are filled with a film of matrix. Thus it appears that some antero-posterior movement may have been permitted between these bones.

The *pterygoids* (figs. 25, 31, 32, 33) are made up of many complex and delicate parts. The quadrate wing of each is a thin broad vertical plate which curves medially along its ventral border to form a thicker quadrate bar reaching into the fossa lying above the medial end of the condyle of the quadrate. Anteriorly this combined plate and bar curls around the smooth, anterior face of the basipterygoid process of the basiphenoid with which it articulates by a smooth, glenoid surface.

From the basipterygoid process antero-laterally, the pterygoid flattens out over the posterior face of the combined palatine and ectopterygoid. Here it extends in a slightly curved plate to the periphery of the ectopterygoid, and embraces the posterior tip of the palatine in a peculiar manner (figs. 34, 35).

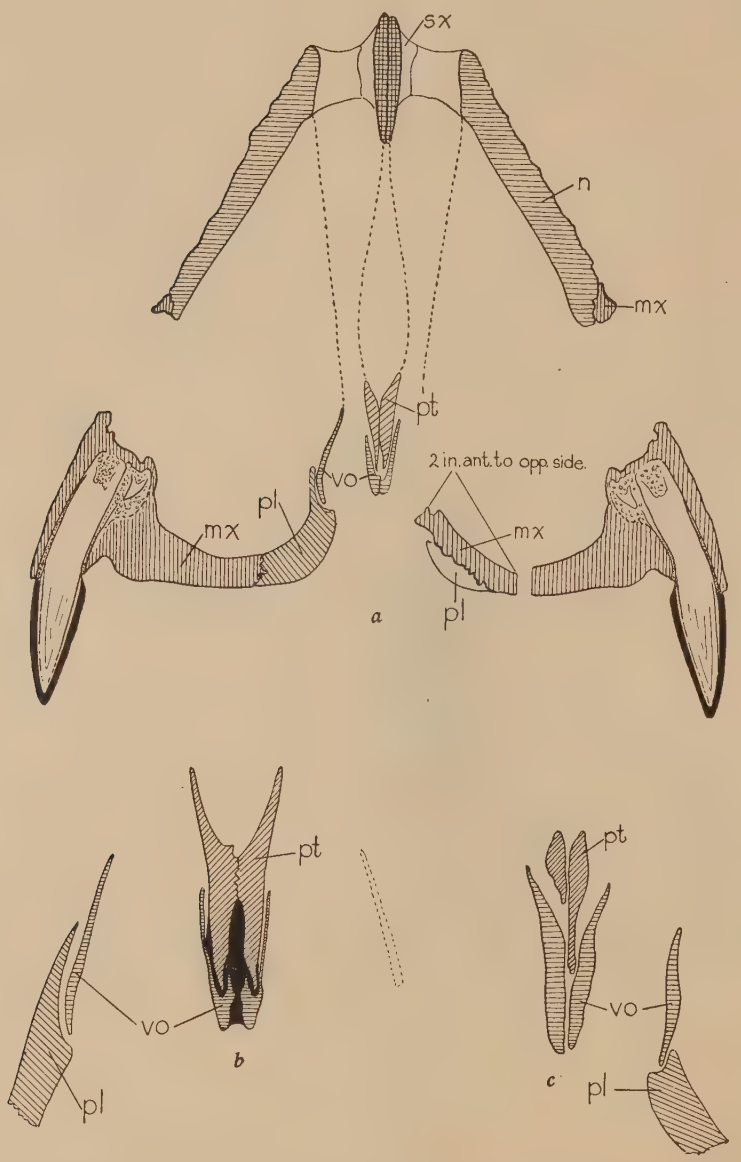


Fig. 32. Transverse sections through internarial septa of *M. adamanensis* (type). *a.* Section of entire skull; dotted lines indicate possible locations of cartilages bounding the narial passages, ×½. *b.* Section through posterior portion of inter-choanal septum, one-half inch posterior to *a*, ×1. *c.* Section through middle of inter-choanal septum, one inch anterior to *a.*; left side, ×1.

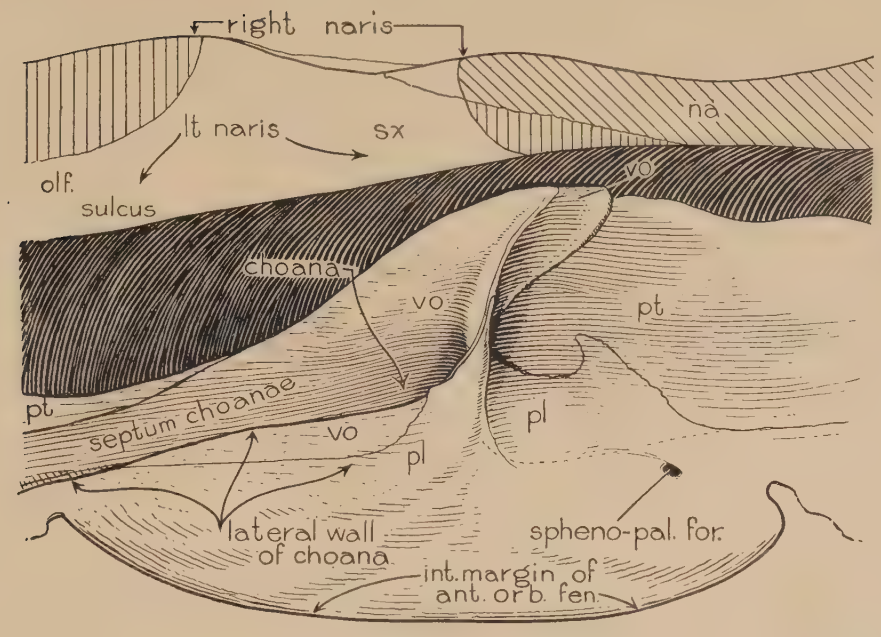


Fig. 33. *M. gregorii* (type), sagittal section of narial region exposing the prevomer-palatine-pterygoid complex at upper margin of posterior borders of left choana. These parts are shown in latero-dorsal view, ×½.

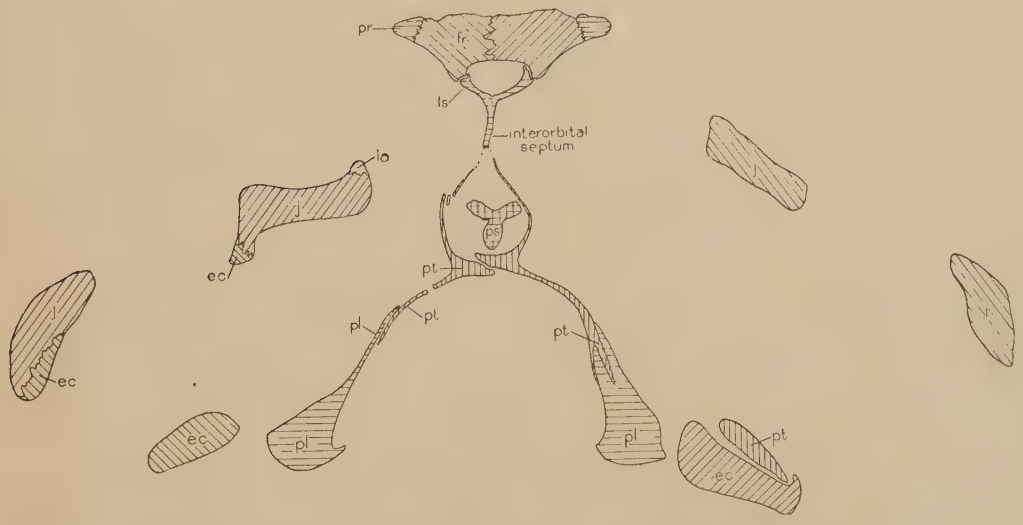


Fig. 34. Transverse section of entire skull of *M. gregorii* (type), through centers of orbits, and anterior parts of lateral temporal fenestra, ×⅓.

Extending dorsally from the basipterygoid condyle is a thick plate of the pterygoid which is continuous with the quadrate wing and which conceals the broad lateral surface of the basisphenoid. This plate bears a shallow groove on its outer (lateral) surface and this groove broadens dorsally to receive the base of the epipterygoid with which it is loosely connected. From the dorsal margin of this plate the pterygoid sends up a buttressed process about 25 mm. long which lies within the concavity of the epipterygoid (fig. 36).

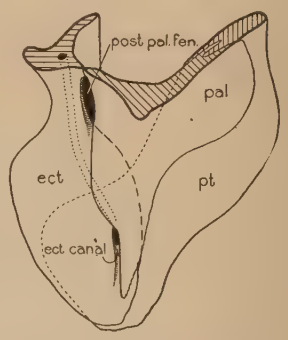


Fig. 35. Ectopterygoid process of *M. gregorii* (type), right side, antero-ventral view, ×½.

Anterior to the basipterygoid processes the pterygoid sends forward an extensive palatal plate which is thickened and rounded along the margins of the narrow interpterygoidal fissure and gradually curves downward becoming thinner laterally, over the lower surfaces of the palatal flanges of the palatines (fig. 25).

The dorsal surfaces of the palatal processes of the pterygoids send vertically, from near their inner margins, a pair of exceedingly thin plates which curve around and over the parasphenoid rostrum to approach the interorbital septum with which they were presumably connected by cartilage (fig. 34). Just behind the choanæ these plates pass between the dorsal buttresses of the prevomers (fig. 33) and join to form the median portion of the inter-choanal septum. In the posterior third of the septum these pterygoidal plates ride in a V formed by the septal processes of the prevomers (fig. 32). Anterior to this point they separate dorsally to form another V the apex of which rests against the dorsal borders of the prevomers and continues, becoming attenuate and delicate, as far as the anterior margins of choanæ, above which they end in two very fine, separated points (fig. 25). These structures have previously been noted by Case (1922) who doubtfully calls them the vomers.

The horizontal palatal plates of the pterygoids join or overlap anteriorly on the mid-line and meet the posterior margins of the prevomers in serrate sutures (fig. 31). Continuing forward around the periphery of the prevomers these plates underlap the palatal flanges of the palatines and end just behind the choanæ (fig. 25).

The palatal plates of the pterygoids are extremely thin at their lateral margins and extend into the deep fossæ above the palatal ridges of the palatines. Posteriorly on each side they join the bar at the base of the ectopterygoid process of the pterygoid and at this point enclose, dorsally, ventrally, and posteriorly, the postero-dorsal borders of the palatines. Although the pterygoids are free from the palatines elsewhere it is highly improbable that this posterior articulation was movable. The union is a close one and contains some slightly roughened limbous sutures (fig. 35).

The *epipterygoids* (fig. 36) are about the size and shape of a large penknife blade. The dorsal extremity of each is a slender, cylindrical rod which inserts

into a deep pit in the postero-ventral margin of the laterosphenoid. This point broadens ventrally into the curved posterior "edge" of the blade. The rounded and thickened "back" of the blade, on the anterior margin is curved convexly forward. The base of the epipterygoid is flattened, forked, and grooved behind.

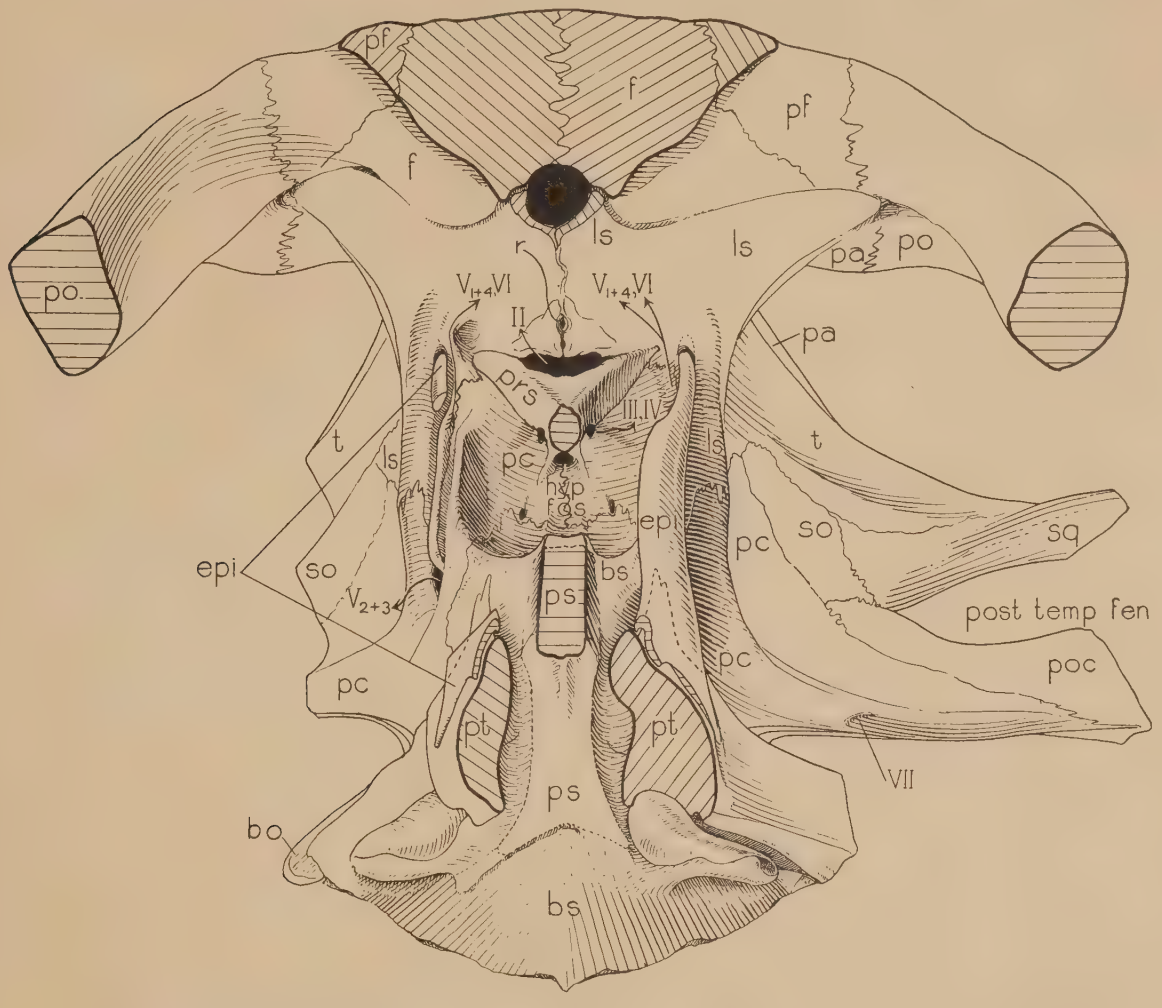


Fig. 36. Anterior aspect of neurocranium of *M. gregorii* (type), ×¾. Sections are on a vertical plane through the posterior borders of the orbits.

Dorsally this groove rides over the posterior vertical ridge of the proötic. At the base of the element the groove encloses the stout, vertical epipterygoid process of the pterygoid. The base sends a broadened, posterior fork postero-ventrally into a shallow depression on the side of the palato-quadrate bar of the pterygoid.

The epipterygoid has about the same extent and position as the pterygoid process of the laterosphenoid in the alligator. Since there is no direct pterygo-laterosphenoid connection in *Machaeroprosopus*, one might regard this process in

the alligator as a vestige of the, already reduced, phytosaurian epipterygoid. It seems possible that the so-called embryological rudiment of the crocodilian epipterygoid is rather a rudiment of the vertical epipterygoid process of the pteryoquadrate bar of the phytosaurs.

The epipterygoid is widely separated from the inner wall of the neurocranium at all points. Likewise, it ends 2 to 3 cm. below the elements of the skull roof. It lies lateral to the origin of the parasphenoid from which it is separated by a space ½ cm. in width. Its relations therefore differ notably from the conditions described in the cynodonts, in which the epipterygoid has been homologized with the alisphenoid of mammals.

The small, weak condition of this element in phytosaurs and its frequent absence in specimens, owing to the looseness of its attachments, make it seem unlikely that it could serve any useful function. It is probably vestigial.

The *laterosphenoids* (figs. 25, 26, 28, 34, 36, 37, 38, 39) are remarkably extensive, paired elements enclosing the elongate and enlarged olfactory tract and a large part of the cerebral cavity. They articulate dorsally with the tabulars, parietals, postfrontals, frontals, and prefrontals; posteriorly with the supraoccipital, epiotics proötics, presphenoid, and epipterygoids; and anteriorly they were doubtless continuous with the sphenethmoid cartilage. The anterior, tubular portion becomes narrow between the centers of the orbits and enlarges again beneath the forepart of the frontals where it provides the floor of a cavity for the olfactory bulbs.

The laterosphenoids send ventrally, between the orbits, a thin vertical plate of bone about 4 sq. cm. in area, which constitutes a bony *interorbital septum* (figs. 25, 34, 37) reaching nearly to the dorsal border of the parasphenoid. This septum was doubtless united to the pterygoids by the supraseptal cartilages. Posteriorly this septum was evidently continued in cartilage as evinced by a roughened ridge on the ventral mid-line of the laterosphenoids. The interorbital septum has no trace of the medial suture which elsewhere separates the laterosphenoids.

The posterior border of each laterosphenoid joins the curved anterior margin of the proötic, sending back a stout process, between this element and the parietotabulare, and a narrow, elongate crest which extends downward into the mouth of the proötic foramen. This ridge bounds laterally a groove which proceeds antero-dorsally from the anterior portion of the proötic foramen, and evidently conducted the first or opthalmic branch of the trigeminal nerve (together with the so-called "fourth" branch to the levator bulbi muscles), and the abducens, through the fissure between the upper part of the epipterygoid and the proötic. This bordering ridge partly divides the foramen into two portions, the posterior of which doubtless gave exit to V_2 and V_3 (figs. 36, 37).

In the ventral mid-line at the posterior end of the cartilaginous interseptum, there is a large horizontal optic fissure bounded above by the posterior midventral margin of the tubular portion of the laterosphenoid (fig. 36). There is a conical pit in the presphenoid within the mouth of this fissure and above its main

canal (figs. 25, 38). The optic fissure is bounded below and separated from the hypophyseal fossa by a trough-like lower lip which projects forward as the spine of the presphenoid. The fissure provides exit for the optic nerves, and the pit, which is separated from the brain cavity by a curved plate of the presphenoid, may have been a receptacle either for a dorsal part of the optic chiasma, the optic commissure, or more probably for a dorsal lobe of the hypophysis (cf. p. 132).

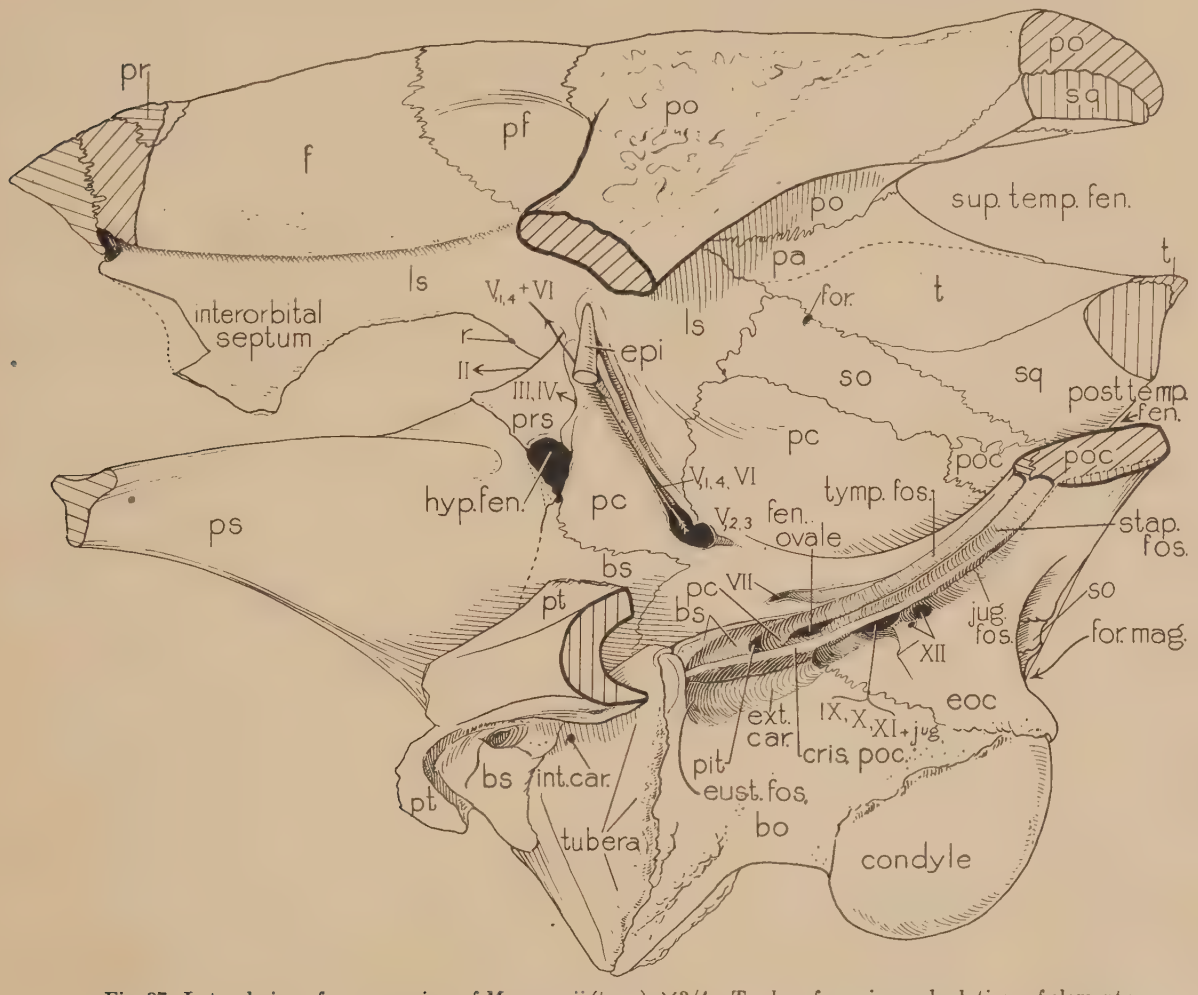


Fig. 37. Lateral view of neurocranium of *M. gregorii* (type), ×3/4. To show foramina and relations of elements on the outer wall of the brain case. *r*=foramen from olfactory lobes to interorbital region. *Cris. poc.*=*crista paroccipitalis*. *Hyp. fen.*=hypophyseal fenestra. *Stap. fos.*=stapedial fossa. *Eust. fos.*=eustachian fossa. *Tymp. fos.*=tympanic fossa. *Jug. fos.*=jugular fossa. *ls.*=laterosphenoid.

In the mid-line, just above the optic fissure is a small foramen (figs. 25, 36*r*), which possibly conducted the nervus terminalis from the cerebral lobes to the organ of Jacobson, but it is much more probable that Jacobson's organ was supplied by a separate nerve from the olfactory bulb and that the foramen in question gave passage to a blood vessel (cf. p. 129).

The laterosphenoids are partly excluded from the inner cranial wall, below the optic foramen, by the inner bulbs of the presphenoid. They appear on the inner wall just in front of the proötics and epiotics (figs. 25, 38).

The *basisphenoid* is a heavy mid-ventral element forming a small portion of the floor and lateral walls of the brain case. It expands ventrally in the vertical plane to meet the basioccipital over a broad, serrate, sutural surface of great strength (fig. 25). Antero-ventrally it articulates, through the enlarged basipterygoid knobs, with the pterygoid (fig. 36). Anteriorly and ventrally it supports the parasphenoid rostrum. It is entirely separated from the presphenoid, which it doubtless joined by cartilage along the anterior wall of the brain case. Remnants of this cartilage are possibly present in the type of *M. gregorii*. Antero-dorsally, the basisphenoid joins the proötics. It does not reach the inner wall of the otic capsule. Postero-dorsally on each side it sends back a short process within the base of the paroccipital arm of the proötic. Its postero-dorsal margin is separated from the basioccipital by a crest of the paroccipital which rises in front of the jugular foramen (fig. 37, *cris. poc.*).

The basisphenoid is excavated into a basin-like depression in the floor of the brain case, which doubtless received the pons varolii (cf. p. 133).

On the anterior mid-line the basisphenoid is hollowed into a large pituitary fossa or sella turcica which lies behind the base of the parasphenoid. This fossa communicates dorsally with a narrow hypophyseal foramen in the presphenoid. The shape of the fossa indicates that the hypophysis was trilobate with a large central lobe, smaller and more slender lateral lobes and a slender, elongate dorsal stem. A pair of foramina extend downward from the apex of the fossa. They leave the basisphenoid on each side in the groove between the basipterygoid process and the tubera. They transmitted the internal carotid artery (figs. 25, 36).

The pituitary fossa communicates with the exterior at the level of the mid-region of the epipterygoids, by large lateral fenestræ. Antero-ventrally it is bounded by a thin spine of the basisphenoid. This spine supports a part of the dorsal base of the parasphenoid with which it appears to be united by suture (fig. 25).

The basisphenoid reaches the internal aperture of the trigeminal or proötic foramen. Postero-ventral to this, at the apex of the process which runs back below the proötic, is a narrow cleft ending in a small foramen. This is apparently the foramen marked VII by Huene (1911, fig. 20). It reaches the inner cranial wall just below the trigeminal foramen, after passing between the proötic and the basisphenoid (figs. 25, 37, 39).

There are no foramina for the eustachian ducts such as there are in the crocodilia. The middle ear in phytosaurs was not enclosed in bone.

The *basioccipital* (figs. 25, 37, 39) comprises a rounded condyle; a stout condylar "neck," which is grooved laterally, and antero-ventral vertical expansions (tubera) which articulate with the basisphenoid. The median posterior surfaces of the tubera are provided with a roughened area for the fasciæ of powerful mid-ventral neck muscles. The lateral knobs are also roughened in a similar way.

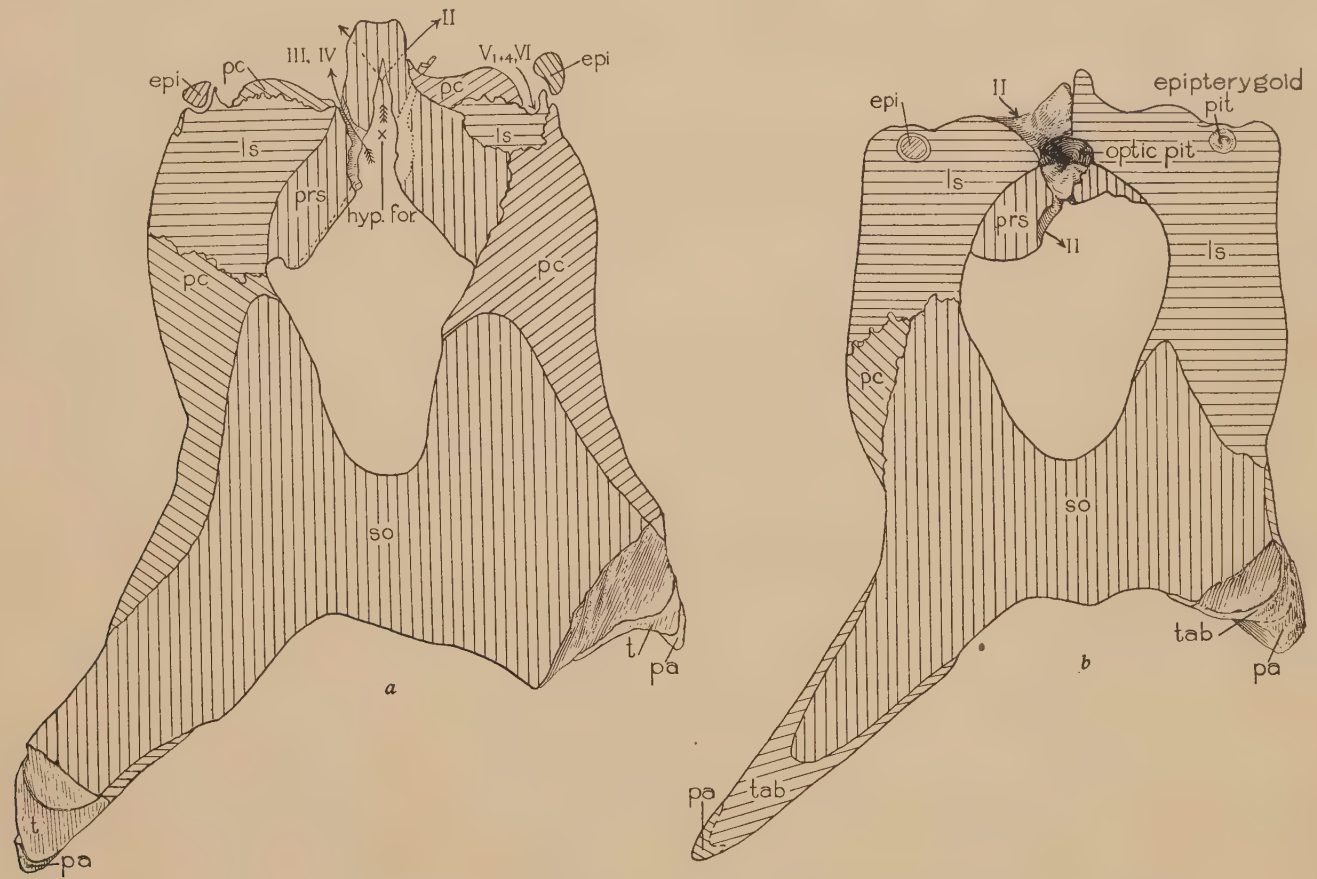


Fig. 38. Cross-sections of brain case of *M. gregorii* (type), ×1. *a*. Frontal (horizontal) section through oculomotor foramen, ventral aspect; left side one-half inch below right. *b*. Frontal section through optic foramen, ventral aspect; left side 1½ inches above left side of *a*, right side one-half inch below left.

Dorsally, the condylar "neck" is entirely excluded from the floor of the cranial cavity by the expanded foot plates of the exoccipitals which rest in roughened sutures upon it (fig. 25).

The articular surface of the condyle is more extensive ventrally than dorsally, permitting more latitude in downward movements of the head than in upward movements. A conical "notochordal" pit penetrates the extremity of the condyle for a depth of 4 mm. and is met dorsally by an indistinct groove which separates the upper half of the condyle into two articular faces. The condyle is almost a perfect hemisphere, of which the exoccipitals form but an insignificant portion.

Antero-laterally the basioccipital adjoins the ventral ridges of the paroccipitals on each side. Behind these is a deep groove leading upward into the jugular foramen (fig. 37). This groove possibly transmitted the external jugular vein.

The *exoccipitals* form the entire floor of the foramen magnum and a considerable area within it. They are separated above by the supraoccipital (figs. 29, 39). Except at their lateral extremities, they are suturally distinct from the paroccipitals, which they adjoin along almost their entire dorsal and anterior surfaces. Each element borders the posterior margin of the stapedial fossa and ends in a thin sheet under the narrow part of the shaft of the paroccipital below the posttemporal fenestra (fig. 37). The lateral sutures with the paroccipital are usually obliterated by fusion. They are close and smooth, but plain to be seen, in a young disarticulated specimen at hand (7307/27159).

Two foramina for the twelfth nerve are excavated in the anterior border of the exoccipital on each side and pass into the outer cranial wall through the front of the exoccipital pillar (figs. 37, 39). They enter the inner cranial wall separately just behind the jugular foramen (fig. 25). The anterior twelfth foramen is smaller and more ventrally placed than the posterior, just as in the alligator.

The exoccipital forms the posterior border of the jugular foramen at the wall of the brain. Outwardly this foramen develops an antero-ventral channel in the basoccipital and a posterior channel in the exoccipital.

The foramen magnum is a little depressed, about half as large as the condyle, and is slightly wider at its aperture than within.

Anteriorly, beneath the medulla, the exoccipitals form a pair of small bulbs which overlap the basisphenoid and exclude the basioccipital from the brain case.

The *paroccipitals* (=opisthotics) are greatly elongated and terminate on each side by a flattened extremity lying against the inner surface of the ventral process of the squamosal. This extremity also gains a ventral sutural contact with the quadrate in this region and a dorsal contact with the two median processes of the squamosal (fig. 30). The narrow portion of the arm forms the lower border of the posttemporal fenestra. Medial to this fenestra the element widens slightly and becomes squarish in cross-section inserting between the supraoccipital and squamosal above, the proötic, in front, and the exoccipital below (fig. 29). It is now lost to view externally except for a ventral strip along the stapedial groove which is formed entirely by this bone. The posterior border of this groove is raised

into a high crest as the cranial wall is approached. This ridge passes downward as a sheet of bone separating the jugular foramen from the fenestra ovalis at the foot of the stapes (fig. 37). Ventrally, its crest then inserts between the lateral margins of the basisphenoid and the basioccipital where it apparently ends. The stapedial groove curves forward slightly at the wall of the vestibule and the strip of the paroccipital which constitutes its floor thickens and protrudes into the cavity of the inner ear as a crenulated process about 10 mm. in diameter (fig. 39).

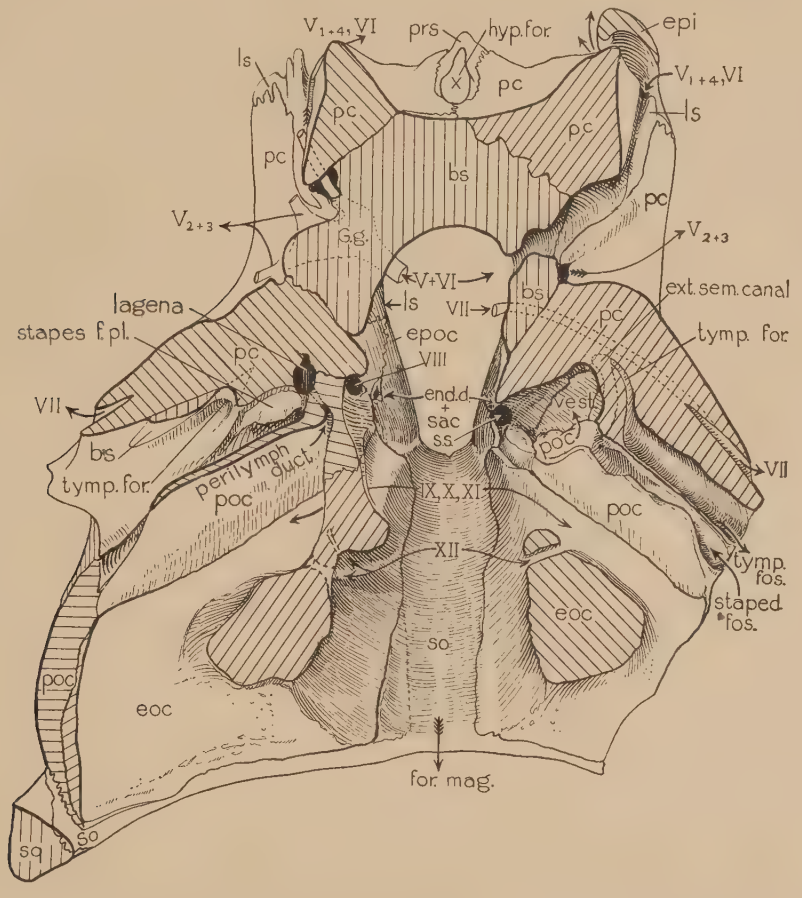


Fig. 39. Frontal section through brain case of *M. gregorii* (type), at level of proötic (V) foramen on left side and one-half inch below it on right; ventral aspect, ×1. *Hyp. for.* = hypophyseal foramen. *Vest.* = vestibule of inner ear. *Ext. sem. canal* = tunnel of external semicircular canal. *Stapes f. pl.* = foot plate of right stapes. *S. s.* = cavity for the superior sinus of the labyrinth. *G. g.* = cavity for the Gasserian ganglion. *ls.* = laterosphenoid.

This process evidently lay above the sacculus and lagena, separating these from the utriculus. From this process a ridge passes inwardly to form a part of the posterior boundary of the internal foramen (nerve VIII). The process probably supported the dorsal border of the membrane of the fenestra ovalis.

The otic arm of the paroccipital is excavated by a tunnel (fig. 40) which enclosed the posterior ampulla, the adjoining portions of the posterior and the horizontal

semicircular canals, and a portion of the utriculus. The horizontal canal is partly excluded from the posterior wall of the vestibule by a small pillar which extends dorsally above the fenestra ovalis and within the arc of the horizontal canal. The antero-median tip of the paroccipital forms the larger part of the roof of the vestibule. It meets the proötic along the margin of the vestibular cavity and lies as a thin sheet between the vestibule and the epiotic (fig. 40).

The stapedial groove continues postero-laterally beneath the ventral margin of the paroccipital as far as the narrowest part of its shaft. Here it gradually dies out. Its direct projection would indicate that the outer end of the *stapes* lay in the groove, formed by the quadrate, beneath the squamosal expansion of the paroccipital, and that the tip of the stapes on the external tympanum lay in the center of the notch just behind the quadrate foramen.

None of our skulls adequately shows any part of the *stapes*. In one specimen (27070) there is a splint-like bone, about 90 mm. long, 10 mm. broad, and ½ mm. thick, lying between the quadrate and the quadratojugal which has been crushed down upon it. This I take to be a section of the outer end of the stapes, which in a large animal would have been about 200 mm. in length and much flattened in cross-section at its outer end, becoming more rounded near the foot plate. In *M. gregorii* the foot plate of the right stapes apparently lies *in situ*, but is so crushed that its details cannot be determined (fig. 39).

The *proötics* form a large part of the anterior and lateral walls of the neurocranium. They are bounded on the inner walls of the brain case by the epiotics, the laterosphenoids, the presphenoid, and the basisphenoid (fig. 25). Each makes up a large part of the anterior median and ventral walls and part of the roof of the cavity of the vestibule (fig. 40). In this region the proötics join the basisphenoid ventrally and anteriorly, the laterosphenoid anteriorly, the epiotics dorsally, and the paroccipitals posteriorly, sending out a process under each arm of the latter. The anterior part of this process extends downward over the side of the basisphenoid.

The proötic bounds nearly the whole external border of the proötic foramen for the fifth and sixth nerves (fig. 37). On the ventro-internal wall of the foramen it meets the basisphenoid (fig. 39). Dorsal to the foramen it joins the laterosphenoid. The supraoccipital receives its postero-dorsal margin (fig. 29).

The paroccipital process of the proötic is excavated into two grooves, the anterior of which presumably conducts the seventh nerve postero-laterally after its exit from the foramen. The posterior groove passes above the foramen ovale and, turning ventrally in a deep triangular pit, continues downward in the side of the basisphenoid (fig. 37).

I have explored this pit (in specimen 27021) and find that it sends a small foramen into the external ampullar cavity (fig. 40).

The proötic encloses a large part of the vestibular cavity, nearly all of the ventrally projecting cavity of the lagena and the anterior portion of the horizontal and anterior semicircular canals.

There are two antero-posterior sutures plainly visible, separating the roof of the vestibular cavity into an inner third (proötic), a medial third (paroccipital), and a lateral third (proötic). (See fig. 40.)

The *epiotics* (figs. 25, 39, 40) are fused to the supraoccipital and are separated by suture from all other surrounding elements. The bone extends ventrally on the inner wall of the brain case to meet the proötic and laterosphenoid. Posteriorly it meets

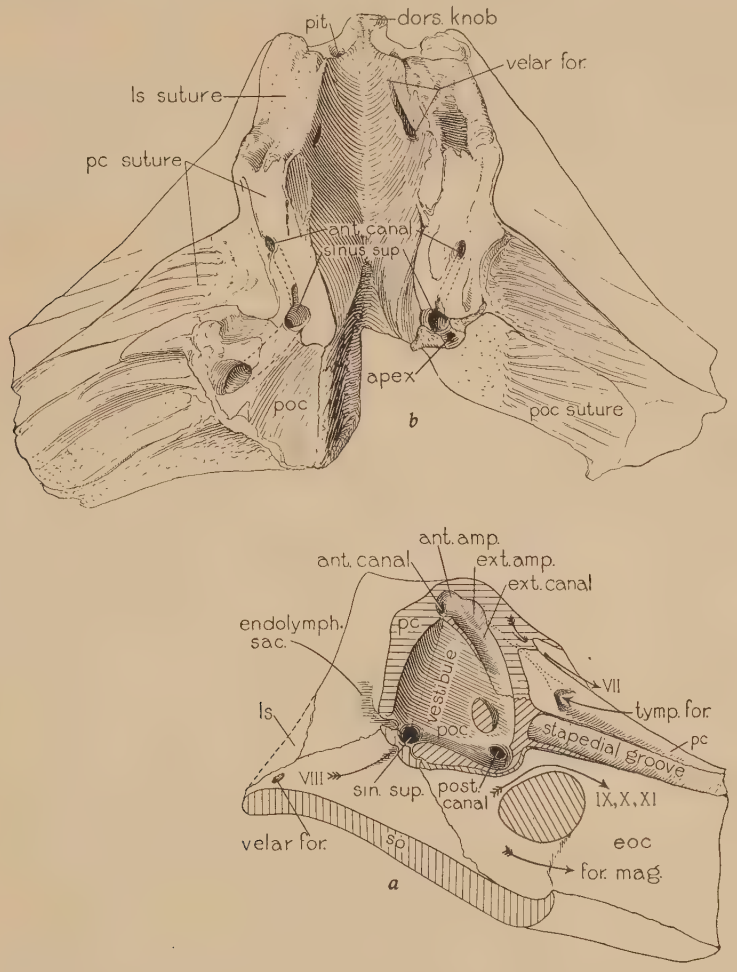


Fig. 40. Parts of skulls of *Machaeroprosopus* showing region of inner ear, ×1. *a*. *M. tenuis*, 7043/27021, frontal section through the left vestibule, ventral aspect; showing tunnel for the external semicircular canal in the proötic and paroccipital, the entrances of the tunnels for the anterior and posterior canals, and the cavity for the endolymphatic sac on the inner wall of the brain case. *b*. A complete dissociated supraoccipital of *M. zunii*, 7307/27159, antero-ventral aspect. A portion of the paroccipital remains joined on the right side.

the paroccipital above the roof of the vestibule. A small foramen and a pit for the endolymphatic duct and sac lie in the posterior portion of its suture with the proötic.

The postero-ventral portion of the epiotic encloses the median portions of the posterior and anterior semicircular canals, and the upper end of the sinus superior of the utriculus with its apex.

The *supraoccipital* (figs. 29, 40) forms the mid-dorsal part of the foramen magnum and the posterior portion of the wall of the brain case. It extends dorsally along the posterior mid-line to meet the parietals, laterally to join the tabulars and squamosals, and ventrally to meet the exoccipitals and paroccipitals. On the outer surface of the lateral wall of the cranium it meets the tabulars, laterosphenoids, and proötics. Ventrally, on the inner cranial wall, it joins the exoccipitals, paroccipitals, and epiotics, being fused with the latter even in young specimens. Anteriorly the proötics exclude it from contact with the basisphenoid.

Much of its posterior surface is concealed in front of the tabulars, and a good deal of its lateral extent lies within the proötics. Its separation from the tabulars is clear.

Its sutures with the parietals and laterosphenoids are roughened but are covered with a glazed film (7037/27159, juv.) as if cartilage persisted on those borders. It articulates with the floor of the parietals by means of a rounded median knob. Its sutures with the proötics are serrate, those with the paroccipitals strongly dentate.

Its dorsal extremity is excavated into a pair of vertical pockets. From the apex of each of these a "velar" foramen passes downward to emerge on the inner surface of the brain case (fig. 40).

The *parasphenoid* (figs. 25, 36, 37) forms the greater part of an elongate rostrum occupying the entire length of the interpterygoid vacuity and terminating behind and above the posterior borders of the choanæ. The vertically compressed base of this rostrum arises ventrally from the basisphenoid with which it is largely fused. The base sends backward a thin ventral plate along the anterior mid-line of the descending process of the basisphenoid. This plate forks slightly at its extremity which lies in the posterior part of the trough between the basipterygoid processes. The base rests in dorsal contact with that portion of the basisphenoid which encloses the base and front of the pituitary fossa. At this contact the dorsal border of the parasphenoid ends in two lateral knobs. Anteriorly the dorsal border expands into a trough, the edges of which approach the dorsal plates of the pterygoid but probably do not touch these except anteriorly (fig. 34).

The dorsal portion of the base of the parasphenoid abuts against the ventral side of the spine of the presphenoid (fig. 25), from which it is separated by a short suture.

The *presphenoid* is an entirely distinct element of singular form. It is separated from the basisphenoid by the excessive elevation of the brain case and hinder part of the skull. Its most peculiar feature is a pair of large knobs that project backward from the sides of the hypophyseal foramen into the brain cavity (figs. 25, 38). These knobs or bulbs adjoin the cranial walls below the temporal lobes of the cerebrum and are grooved to accommodate the third and fourth nerves. Dorsally these knobs join on the mid-line and form a plate which separates the "optic pit" from the brain. They push through the anterior wall of the neurocranium, between the antero-dorsal processes of the proötics, and form a trough-

like shelf which underlies the optic fissure. This trough has a large mid-ventral hypophyseal foramen. Lateral to this, in the suture between proötic and presphenoid, there is a small foramen, on each side, which possibly transmitted nerves III and IV (or at least one of them). This foramen arises close to the hypophyseal foramen on the inner wall.

The presphenoid spine meets the dorsal base of the parasphenoid (fig. 25), but is not extended along it in the way Huene (1911) has described in *Mystriosuchus*.

The *prevomers* (figs. 25, 31, 33) are of the primitive reptilian type, differing widely from the crocodilian form. They meet the pterygoids posteriorly, overlapping them slightly in well defined serrate sutures (shown best in 26699 fig. 31). On the mid-line this union occurs 60 mm. behind the choanæ. Here the prevomers spread out over the palate, their lateral borders being encircled by the pterygoids and their dorsal surfaces lying below the dorsal plate of the palatines. The palatal expansions of the prevomers pass upward behind and around the posterior borders of the choanæ and spread out dorsally over the sides of the vertical plates of the pterygoids, forming a supporting buttress for these plates and a pillar separating these plates from the palatines (fig. 33). This dorsal process of the prevomer has been regarded by Huene (1911*b*, figs. 5, 6) as part of the pterygoid, and by Case (1922, fig. 26) as part of the palatine.[6]

The prevomers cover the palatal border of the interchoanal septum for its entire length, and they extend upward on each side of the septum encasing the median pterygoidal portion of the posterior third of the septum in a thin sheath (fig. 25). This is the condition in the type of *M. gregorii*. In the type of *M. adamanensis* the prevomers form a much smaller part of the lateral surfaces of the septum (fig. 32); their relations to the pterygoids are the same, however, in the two specimens.

The prevomers send thin processes along the lateral margins of the posterior half of the choanæ. These processes are supported laterally by equally thin plates of the palatines which reach the antero-lateral margins of the choanæ (figs. 25, 33).

Anterior to the septum the tips of the prevomers slip between the palatal processes of the premaxillaries and the median palatal portions of the maxillaries. They do not meet the palatines in this region: they insert into pits in the maxillaries (fig. 25).

The *palatines* form the ventral and lateral portions of the palatal vault (figs. 25, 34). Each has a stout thickened axis extending from the inner margin of the transverse to the level of the anterior border of the choanæ. Lateral to this axis a thinner horizontal plate meets the palatal shelf of the maxillary and underlaps it slightly. The external border of this plate also surrounds the median periphery of the palatal foramen, which is small in *Machaeroprosopus* (fig. 35).

[6] See also Case, *Mem. Univ. Mich. Mus.*, vol. 2, 1929, pp. 32–37; received after the above account was written. Case now regards the entire post-choanal buttress as composed of an upraised process of the palatine. In neither of our specimens do I find an anterior suture between this buttress and the prevomer; otherwise our views of the structure of the palate are nearly in accord.

The dorsal flange of the palatine is a thin, delicate, plate which borders the antero-lateral margin of the choana and domes upward and inward over the lateral surfaces of the prevomer and pterygoid. It reaches its maximum dorsal extent in the region of the prevomerine buttress over the edge of which it rests, in a thin point (fig. 33).

The axis of the palatine, along the posterior half of its extent, sends out a low, sharp, medial ridge which forms an incipient secondary palate. It has been thought that perhaps this ridge was continuous with its fellow by a cartilaginous sheet closing the palatal vault. Since the ridge rises to the level of the choana at a point about two-thirds of the way forward on the margin of the latter it is probable that such a sheet would have been continuous across the anterior third of the choanal openings.

The internal choanæ are much larger than the external, hence much larger than necessary merely for passage of air. The lower margin of the choanal septum dips forward in the anterior portion of its extent in direct projection of the line of the medial palatal ridges. In the anterior region the septum is flattened below and much thickened as if to resist the pressure brought upon food in the mouth. In the posterior region the septum is delicate, sharply edged, and inclines upward. The anterior portion of the septum is provided with a knob posteriorly and overhanging edges (fig. 25).

I think all this indicates that the anterior third of the enormous choanæ was covered in some way with cartilage or connective tissue, with a probability that a well developed Jacobson's organ reached the palate here. It is also likely that this covering was continued posteriorly by cartilaginous extensions or lappets projecting at least part way across the palatal vault, partly enclosing the air passage and protecting the delicate bones on the roof of the vault.

The axis of each palatine bone is deeply scarred and grooved in *M. gregorii*. This was possibly caused by the friction of rough food.

Each *ectopterygoid* (=transverse) sends a dorsal finger along the medial spine of the jugal, and an anterior process along the lower margin of the jugal below the posterior angle of the antorbital fenestra (fig. 34). This latter process also joins the posterior alveolar border of the maxillary. The ventral process of the ectopterygoid curves medially, posteriorly, and ventrally from these unions to spread out in a smooth plate over the dorsal face of the ectopterygoid process of the pterygoid. Antero-laterally it joins the palatine in a strong roughened suture. The tip of the palatine is separated from the tip of the ectopterygoids by a groove in the latter which leads into a foramen traversing the entire length of the bone, crossing the upper jugal suture, and joining the infraorbital canal within the inner spine of the jugal. This foramen possibly transmits a branch of nerve V, innervating the pterygoideus muscles. It might be called the ectopterygoid canal (fig. 35).

BONES OF THE LOWER JAW

The most nearly complete figure of the lower jaw of a phytosaur is that by Huene (1911*b*, fig. 113, *Mystriosuchus plieningeri*). The structures he indicates are approximately the same as those of *Machaeroprosopus* except that in the latter there is only one accessory internal fenestra and this is much larger than in *Mystriosuchus*. Also, the prearticulare is suturally distinct from the articulare in our material and *the coronoid can be demonstrated as a distinct element* on each side.

The specimens used in the following descriptions include the complete lower jaws of 7034/26688, 7037/26699, 7043/27018, 7050/27031, and A272/27200, also the dissociated elements of 7037/27070, 7307/27159 and several specimens which include only symphyseal portions of the rami.

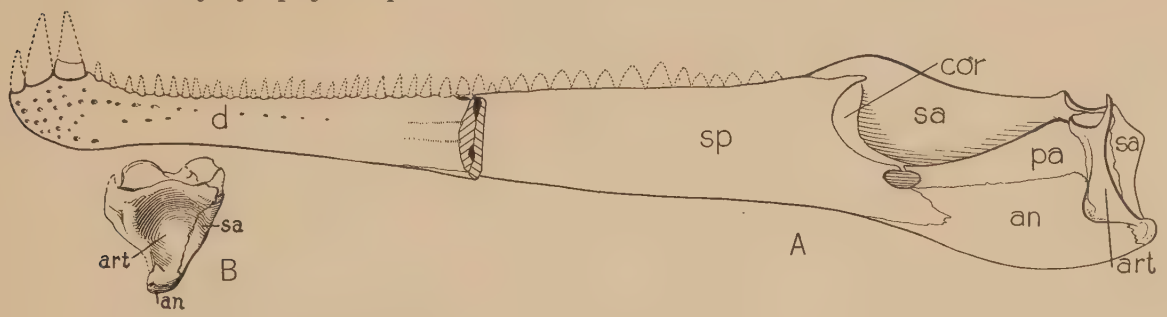


Fig. 41. Lower jaws of *Machaeroprosopus*, ×1/9. *a. M. lithodendrorum* (type), posterior ramus of left side cut away to show median side of right ramus. *b. M. adamanensis* (type), posterior view of right ramus.

The *articulars* (figs. 41, 44) are greatly expanded both vertically and laterally. Each furnishes only about three-fourths of the area of the enlarged glenoid surface; the lateral fourth of the glenoid being excavated in the surangulare which joins the articulare in strong serrate sutures (27070). A pronounced groove is present across the glenoid at the line of union of these elements.

The articulare meets the prearticulare over a large part of the medial (internal) surface of its own anterior (Meckelian) process, and likewise along the dorsal border of this process. The sutural surfaces of this process are roughened and glazed having the same appearance as the parietal and proötic sutures of the supraoccipital. The extreme tip is granular and blocks the posterior end of the floor of a Meckelian sulcus 8 mm. in width (in 27200). This width doubtless represents the diameter of *Meckel's cartilage* at its union with the tip of the articulare. *Meckel's cartilage* undoubtedly lay in the muscles penetrating the mandibular fenestra just as it does in the alligator.

A peculiar feature of the articulare is the development of a delicate, vertical process at the postero-internal margin of the glenoid (27200). This process is usually broken away in specimens and has not previously been noted. In front

of the base of this process is a large foramen penetrating the internal ridge of the articulare and continuing dorsally and anteriorly as deep grooves. Evidently this foramen transmitted a posterior cutaneous branch of V_3. The course of the anterior branch of this nerve is indicated by a groove in the angulare.

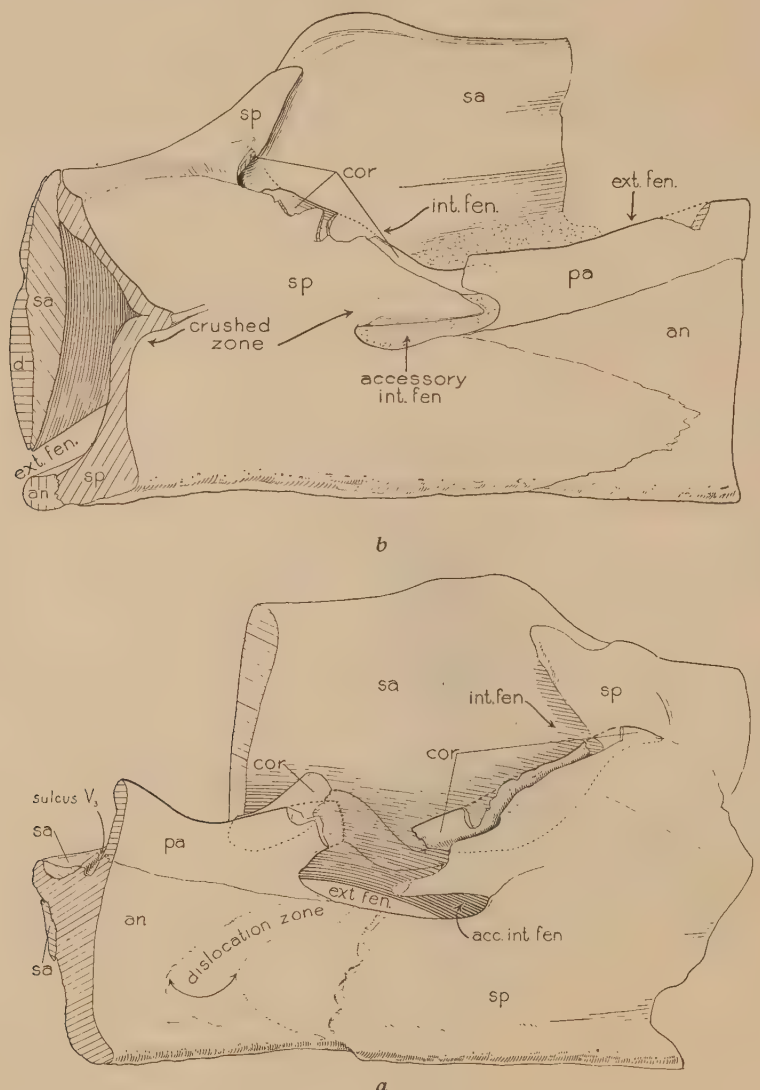
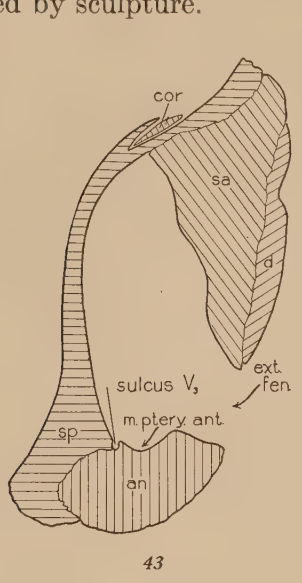


Fig. 42. Sections of lower jaws of *M. gregorii* (type), A270/27200, ×½. *a*. Mid-section of left ramus, internal view, showing relations of vestigial coronoid. Proximal end of coronoid and prearticular displaced. *b*. Mid-section of right ramus. *Sulcus* V_3 = conduit for mandibular branch of V_3.

The *prearticulars* (figs. 41, 42, 44) are of small size. Each sends a slender process forward to the dorsal border of the accessory internal fenestra where it lies against the medial side of the posterior process of the coronoid, barely meeting the thin tip of the splenial (fig. 42).

The postero-dorsal border of the prearticular folds over the dorsal border of the Meckelian process of the articular (fig. 44). The ventral border meets the angulare in a roughened suture and slightly overlaps it on its internal side. The Meckelian sulcus is excavated in the prearticulare and the latter meets the surangulare on the lateral margin of this groove.

The *angulars* (figs. 11, 41, 42, 43) are elongate and do not quite reach the posterior borders of the jaws. Posterior to the external fenestra about half of their extent lies medial to the broad surangulars, to which they are firmly united by serrate sutures. Their lateral surfaces and ventral borders are moderately roughened by sculpture.



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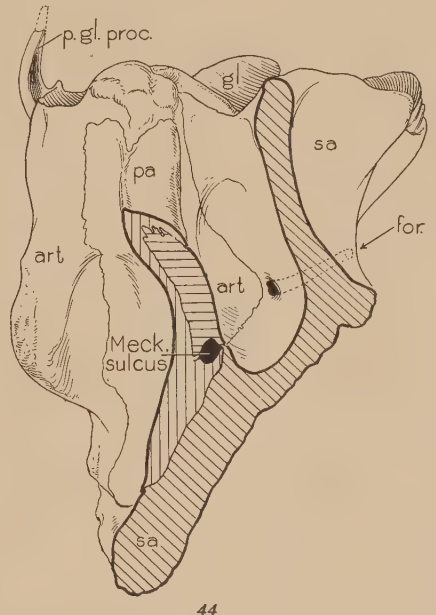

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Fig. 43. Section of right ramus of lower jaw of *M. gregorii* (type), through distal end of coronoid, ×½.

Fig. 44. Posterior part of right ramus of lower jaw of *M. gregorii* (type), showing relations of articulare, prearticulare, and surangulare, ×½. *P. gl. proc.*=post-glenoid process; *Meck. sulcus*=pit at union of Meckel's cartilage and articulare; *for.*=foramen for cutaneous branch of V_3, passing backward and outward through the surangulare.

The *surangulars* (figs. 11, 41, 42, 43, 44) have the external appearance of a large dermal scute, a resemblance which is heightened by the presence of a deeply sculptured external longitudinal comb. Each enters the glenoid and forms about a fourth of the area of the posterior face of the mandible, failing however to reach the tip of the lower, hook-like process of the articulare.

The surangulare forms the highest part of the "coronoid" process, just in front of which it meets the splenial and the dentary. It is penetrated by a foramen which enters the external surface below the glenoid and passes forward and inward to appear in the deep groove of the surangulare lying lateral to the articulare and the Meckelian sulcus. Its anterior point, inserted between the dentary and splenial, forms the posterior border of the hindmost alveolus, and extends forward beneath several of the other alveoli.

The *splenials* (figs. 11, 41, 42, 43) are of great size. Each forms a large part of the internal border, about one-half of the ventral border, and an equal amount of the symphysis of the ramus. Each forms the inner margin of all the alveoli behind the symphysis and four of those adjacent to the posterior portion of the symphysis as well.

The upper posterior margin of the splenial is extended in a thick point nearly to the tip of the highest point of the surangulare. Below this point it becomes thin and meets the dorso-anterior border of the coronoid. The two elements form the anterior border of the internal fenestra and together comprise most of the delicate bar lying between the internal fenestra and the accessory fenestra (fig. 42).

The *coronoids* (figs. 41, 42, 43) are small, delicate, and somewhat loosely attached to the splenials and the prearticulars. They are doubtless vestigial and are usually lost in specimens. They are well shown only in the type of *M. gregorii* (27200, fig. 42) but also appear in 26688 and 26699. Each lies partly concealed beneath and lateral to the fenestral border of the splenial, inserted in a groove in the inferior border of the postero-dorsal process of the latter and extending as a thin plate around the front of the internal fenestra. The posterior process of the coronoid forms the dorso-internal half of the bar between the internal and accessory fenestræ and terminates on the lateral surface of the anterior point of the prearticulare.

The *dentaries* (figs. 11, 41, 42, 43) are greatly elongated and terminate in swollen extremities containing three enlarged alveoli on each side. The anterior of these is considerably smaller than the other two and the third is the largest. The dentary forms the posterior border of the external fenestra and is separated from its fellow along the posterior portion of the symphysis by the splenial.

MECHANICS OF THE SKULL

A search for the possibility of kinetism in the skull of *Machaeroprosopus* reveals some puzzling things. I have studied all the sutures carefully to consider possibilities of movement and I have examined a number of slightly crushed skulls to discover displacements.

The most frequent displacements are those found between the paroccipital extremity and the ventral process of the squamosal, between the pterygoid and the basipterygoid process of the basisphenoid, and between the palatal plate of the pterygoid and the dorsal plate of the palatine. The quadrates are frequently wrenched out of position in various directions but this always involves a bending or fracture of the quadratojugal arch or other parts. The tubular portions of the laterosphenoids, which articulate beneath the frontals, are often found displaced.

Dissociated skull elements show that all the sutures in the skull roof are strongly serrate with the exception of the naso-septomaxillary union which has no importance in this connection. The sutures in the quadratojugal and postorbito-squamosal arches are also fast. The supraoccipital is immovably fixed to the parietals

as well as to the elements of the brain case. The quadrates are immovably joined to the quadratojugals and to the paroccipitals. The squamosals establish firm unions with the quadrates and the quadratojugals in the upper posterior border of the lateral temporal fenestra. This means that any movement of the quadrate, through the condyle which persists in the ventral pit of the squamosal, would involve a bending of the quadratojugal process of the squamosal and of the narrow portion of the quadratojugal arch. I do not see how such a movement could have been permitted.

At the posterior end of the skull I find that the supraoccipital and squamosal are closely united and that the paroccipital is bound to the exoccipital, the supraoccipital, and the quadrate. How then could there have been any normal movement of the smooth squamoso-paroccipital surfaces?

The basisphenoid, basioccipital, proötics, laterosphenoids, epiotics, and exoccipitals are united by closed sutures, although the first two are often found dissociated. The laterosphenoids are joined to the parietals and tabulars by serrate sutures although more or less free from the postfrontals and frontals.

The palatines, maxillaries, and ectopterygoids are strongly united, the jugals and ectopterygoids as well.

The tabulars are firmly joined to the parietals and squamosals, consequently their smoother supraoccipital surfaces cannot be considered as mobile.

We have yet to consider the pterygoid—prevomer complex. The most obvious articular union in the skull is that between the pterygoid and the basipterygoid process. I have previously described this. The pterygoids and prevomers are united by interlocking dentate sutures except in the choanal septum. They must therefore have moved, if they moved at all, as a unit. All the extensive surfaces between the pterygoids and quadrates are smooth and might have permitted antero-posterior and dorso-ventral movements. This could certainly be said of the overlapping between the palatal plates of the pterygoids and the dorsal plates of the palatines. The prevomer-palatine connections would also have allowed movement in these directions. The prevomer-premaxillary connection is a smooth one, also the ectopterygoid-pterygoid union. The anterior tips of the vomers are loosely encased in the maxillaries (fig. 25).

There is a critical point, however, at which the pterygoid-prevomer unit is fixed to the skull; viz., where the *ectopterygoid processes of the palatines join the pterygoids in roughened, slightly pitted sutures* (27200, fig. 35). This prevents us from building up an interesting case of kinetism in *Machaeroprosopus*. We must regard the skull as akinetic, as Versluys has already found it to be in the European phytosaurs. The indications are that this akinetic condition has been recently acquired, that some close ancestors of our forms were kinetic to the extent, at least, of an independently movable pterygoid, and it also seems possible that at a more distant time the quadrates and the neuro-cranial elements were mobile.

It is likely that an independent movement of the pterygoids is a final stage of kinetism which so far as I know has not yet been observed in reptiles. Versluys

(1927) in a review of the "streptostyly problem" classifies the various forms of kinetism but does not mention this stage, which is an interesting one from the functional standpoint. I should suggest for it the term *parakinetic*. It would be intermediate between the mesokinetic stage of dinosaurs, and the akinetic phytosaurs and the crocodiles which retain the musculature of a kinetic skull in the embryo.

Case (1922) in his study of *Leptosuchus*, a more primitive form than *Machaeroprosopus*, discovers kinetism in the quadrate, occipital, sphenoidal, and pterygoidal segments but does not give convincing evidence.[7] Parakinetism, at least, will doubtless be found in the early phytosaurs.

Since the pterygoids and vomers are edentulous, there would seem to be no advantage in their independent movement so far as swallowing acts are concerned. There are, however, ventral ridges on pterygoids which may take the place of teeth in forcing large struggling prey into the gullet. In *Machaeroprosopus* these structures are stout, curved ridges projecting into the vault between the ectopterygoids.

The muscles concerned with pterygoidal movements have been studied by Lakjer (1926). They are constrictor I dorsalis derivatives innervated by the fourth branch of the "trigeminal" nerve, which also runs to the levator bulbi muscles. They arise from the neuro-cranial walls and the ventral surfaces of the skull roof in lizards and are inserted upon the pterygoid in two groups—the levatores, pterygoidei and the protractores pterygoidei. They are apparently homologous in amphibians, fishes, and various lizards. They are found in the embryo crocodile and disappear in the adult.

These muscles act upon the movable pterygoids (and all united structures) carrying them forward and upward. The opposing downward and backward pull is accomplished by the much stronger pterygoideus muscles inserted on and into the lower jaw.

It is conceivable that this mechanism functioned in a parakinetic skull during deglutition. Living prey, to be swallowed whole, would be seized by the jaws, turned in the proper direction, and then forced into the gullet by small but powerful movements of the pterygoids which could operate while the jaws remained closed, or nearly so.

Anyone who has noticed the difficulty with which a lizard or snake engulfs a large object will perhaps question Versluy's conception of the adaptational significance of kinetism. He suggests the value of the additional gape which the usual forms of kinetism afford. The added gape is slight at best and in a parakinetic skull would not be increased in the least. My suggestions would be that kinetism was developed to furnish a powerful swallowing lever; that in amphikinetic and mesokinetic reptiles the independent mobility of the snout is a release mechanism allowing the prey to be drawn back from the teeth without widely opening the jaws; and that in certain birds specialized habits of food manipulation and possibly preening movements have accompanied this independent mobility of the beak.

[7] See also Case, *Mem. Univ. Mich. Mus.*, vol. 2, 1929, p. 14.

THE INNER EAR

The architecture of the bony parts of the inner ear is shown in four specimens: 7307/27159, *M. zunii*, dissociated supraoccipital and paroccipital exposing the bony labyrinth (fig. 40); 7043/27021, *M. tenuis*, exoccipital, supraoccipital, proötic, and paroccipital exposing the bony labyrinth and a horizontal section of the vestibule (fig. 40); A270/27195, *M. gregorii*, showing vestibule and foramena; A270/27200, type skull of *M. gregorii*, sections of the complete neuro-cranial wall exposing the vestibule, subsaccular process of paroccipital, lagena, foramina, and other features (fig. 39). Enlarged drawings of the vestibular cavity and the bony horizontal canal of *M. gregorii* (type) have been completed from parts exposed in other specimens. Using this composite picture as a guide, a plasticine model has

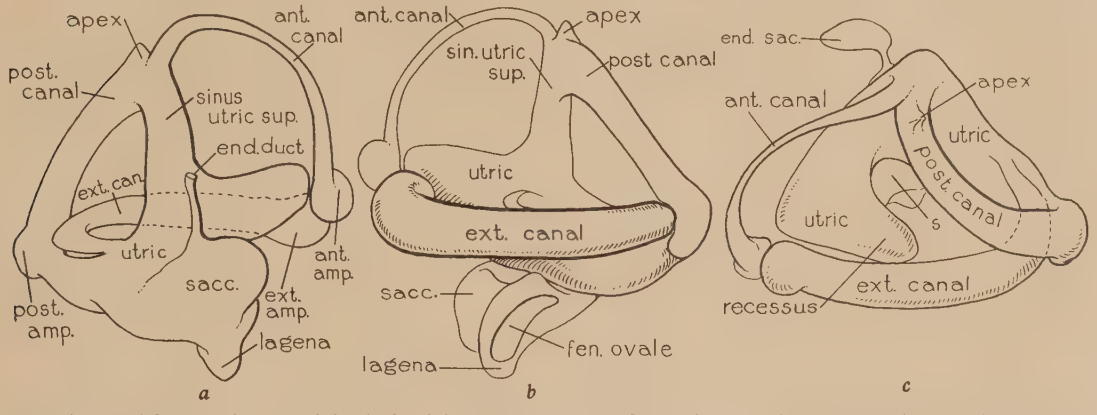

Fig. 45. The membranous labyrinth of *Machaeroprosopus*, drawn from a plasticine model based upon the bony parts preserved in four specimens, ×1. *a*. Left side inner view. *b*. Left side outer view. *c*. Left side dorsal view. See also figs. 39 and 40.

been constructed showing the membranous parts as they would have appeared had they completely filled the various cavities (fig. 45). The supposition that they filled the cavities may lead to errors in the reconstructions.

The relations of the semicircular canals are very definitely shown since these were almost completely enclosed in separate bony tunnels. The external or horizontal canal was the largest of the three in diameter, and lay with its anterior third within the proötic and its posterior two-thirds within the paroccipital bone. It passed about 4 mm. above the inner end of the stapedial groove and its ampulla lay in an enlarged space separated by a very thin, bony wall from the apex of the vestibule. Just behind the ampulla its bony tunnel communicates for a short distance with the outer margin of the vestibule. Its posterior extremity was evidently curled forward in a tail-like funnel which probably lay free in the posterior utricular cavity and doubtless joined the utriculus. The central portion of the external canal shows only a slight curvature.

The posterior canal lay entirely within a round tunnel, the postero-lateral three-fourths of which are enclosed by the paroccipital bone. The anterior fourth, which lay within the epiotic portion of the supraoccipital, bore dorsally, at its apex, a conical process represented by a pit in the bone at this point (fig. 40). The ampulla of the posterior canal is not represented by a corresponding enlargement in the apex of the tunnel and was evidently of small size. The canal itself was shorter and slightly smaller in diameter than the external canal.

The tunnel for the anterior canal is clearly demonstrable in *M. zunii* (fig. 40) and is of exceptionally narrow diameter. It is also compressed in the vertical plane. This canal left the superior sinus of the utriculus at a slightly higher level than did the posterior canal. Its posterior half was enclosed within the ventral part of the epiotic portion of the supraoccipital from which it passed forward, downward, and slightly outward into the proötic, where its ampulla adjoined the ampulla of the external canal. The mid-part of the tunnel for this canal lies about 10 mm. above the roof of the vestibule.

The sinus utriculus superior was vertical, about 5 mm. in length to its union with the posterior canal, and slightly larger in diameter than the external canal. Its apex lay in the epiotic, from which it passed ventrally to enter the postero-internal corner of the vestibule between the extremities of the paroccipital and the proötic, and very near the anterior margin of the exoccipital.

The vestibular cavity is roughly the shape of an inverted triangular pyramid. Its roof is flat and formed by the proötic and paroccipital. Its antero-external face reaches the external canal. Its postero-lateral face is interrupted by a crenulate subsaccular process of the paroccipital, and this process almost completely separates the cavity into a large dorsal (utricular) portion and a smaller ventral (saccular and lagenal) portion. It is evident (type *M. gregorii*) that the lagena was not elongate and perhaps not well differentiated from the sacculus. The presence of a small foramen penetrating the cranial wall near the base of the superior sinus of the utriculus indicates an endolymphatic duct which leads to a sac adjoining the wall of the brain. The duct had a length of about 5 mm. The sac lay in a depression about 3 mm. in depth and 6 mm. in height.

The *eighth nerve* entered the vestibule through a single foramen which lies between the proötic and paroccipital. Just behind and below it a small perilymphatic foramen connects the saccular cavity with the jugular foramen (fig. 39).

The position of the fenestra ovalis is indicated in figure 45*b* by an ellipse drawn on the side of the lagena.

Comparisons.—The inner ear is shut off from the brain wall more completely in phytosaurs, crocodilians, lizards, birds, and mammals than in many other primitive reptiles and amphibians (cf. Watson, 1916). In *Eryops, Diadectes, Diopeus,* and others, the so-called internal auditory meatus or fenestra vestibuli is an opening nearly as large as the diameter of the vestibular cavity. In *Erythrosuchus, "Belodon," Machaeroprosopus, Plateosaurus, Iguanodon,* phytosaurs and crocodiles, which are allied in other respects, the inner ear communicates

with the brain cavity by the narrow acoustic foramen and usually by the endolymphatic duct. The otic bones have almost completely enclosed the inner surface of the vestibule in these forms.

Cope and Case (1914)[8] have attempted reconstructions of the labyrinth of three genera of Permian reptiles, *Diadectes*, *Edaphosaurus*, and *Dimetrodon*. Their restorations seem to show that the bony semicircular cavities are entirely confluent with the bony vestibular cavity in these genera. If this was so it was a marked digression from the conditions in many fossil and modern fishes, amphibians, and reptiles, and Watson's (1916) restoration of the inner ear of *Diadectes* casts doubt upon Cope's earlier interpretation.

Case describes, in *Edaphosaurus* and *Dimetrodon*, an *apex sinus utriculus superioris* such as Retzius has found in certain fishes but not in modern amphibians and reptiles. An apex of this sort occurs in *Machaeroprosopus*.

The following genera of fishes, figured by Retzius, possess an apex, at the dorsal end of the sinus superior, similar to that which is seen in *Machaeroprosopus: Chimaera* (very large), *Protopterus*, *Amia*, *Salmo*, *Scomber*, *Melapturus*, *Perca*, *Raniceps*, *Belone*, and *Anarrhicas*.

In descriptions of the inner ear of therapsids by Sollas and Sollas (1913) and Watson (1913), the vestibule is found to be large, and the lagena in *Diademodon* (Watson) is "long, anteriorly-internally directed and bent." Watson also states that the vestibule is more ventrally located than in primitive reptiles. It is slightly more ventral in position than in *Machaeroprosopus*. The fenestra ovalis is much smaller in *Diademodon* than in *Machaeroprosopus*, and the apex is not definitely present on the sinus superior in *Dicynodon*.

The inner ear of *Machaeroprosopus* is in some respects more primitive than in crocodilians. Comparisons with figures and descriptions by Hasse and by Retzius indicate that the form of the lagena is like that of *Sphenodon*, turtles, and lizards in its blunt, rounded form. In the crocodilians the lagena is elongate and bird-like.

The form of the external canal in *Machaeroprosopus* is more like that of turtles, lizards, and crocodilians than of *Sphenodon*, in which the posterior loop of the external canal passes above and well behind the posterior ampulla.

The relatively small, ventrally placed sacculus of *Machaeroprosopus* has its counterpart in the sacculus of crocodilians, the gecko *Platydactylus*, iguanids, and turtles, and differs widely from the condition in scincs, anguids, lacertids, and serpents, where the sacculus is balloon-like and much enlarged dorsally.

The sinus superior of *Machaeroprosopus* is more slender and elongate than in certain genera of modern turtles.

The modern amphibians appear to differ from the reptiles (including *Machaeroprosopus*) in the rudimentary division of the sacculus and lagena. This is a point, however, that cannot be clearly demonstrated in our material.

[8] Case, in *Jour. Comp. Neurol.*, vol. 45, 1928, pp. 162, 167–168, describes the inner ear of a phytosaur. I had not seen this paper before the closure of my present manuscript.

In conclusion it may be said that the high specialization of the lagena, as seen in crocodilians, is not present in *Machaeroprosopus* although in some other respects the structures are similar. Closest resemblances appear to be with the primitive lizards (geckos and iguanids), and the resemblance here may simply be the retention of primitive reptilian characters in each group.

Peculiar characters of *Machaeroprosopus* include the attenuate character of the anterior canal, the great lateral breadth of the labyrinth, and the large size of the horizontal canal.

THE MIDDLE EAR

The tympanic cavities were not enclosed in bone. Their bony portions are represented solely by the stapedial fossa and a similar groove anterior to and paralleling it which I have called the tympanic fossa (figs. 37, 40). This groove is separated from the stapedial fossa by a low ridge which may have borne a cartilaginous or membranous septum.

The tympanic fossa leads into a funnel-like pit lying just behind the fenestra ovalis. A small foramen (fig. 39, *tymp. for.*) connects the bottom of this pit with the cavity for the ampullæ of the external semicircular canals. In *Trionyx*, according to Ogushi, a foramen in this position continues on through the inner ear and emerges on the dorsal surface of the proötic, transmitting the posterior temporal artery.

Comparisons.—The middle ear of modern crocodilians is enclosed in a complex bony tympanic cavity and the eustachian ducts pass from this into the throat through bony tunnels. These structures are not enclosed in bone in *Machaeroprosopus*, which presumably represents, in this respect, a more primitive stage.

THE BRAIN

The material which I have used in an attempt to reconstruct the brain includes the following specimens: A270/27200, type skull of *M. gregorii*, entire lower neurocranial cavity exposed in three horizontal sections (figs. 25, 38, 39); 7037/27159, *M. zunii*, dissociated parietals, frontals, laterosphenoids, and supraoccipital (fig. 40) showing epiphyseal fossa, cavities for anterior processes of cerebrum, posterior olfactory region, velar foramina, and other features; A270/27195, *M. gregorii*, cranial roof, showing paraphyseal pockets, anterior cerebral pockets, epiphyseal fossa, and anterior olfactory region; 7038/27070, *M. adamanensis*, frontals and parietals showing epiphyseal fossa, cerebral pockets, and olfactory bulb (figs. 26, 28) 7034/27181, *M. lithodendrorum*, showing position of vestigial pineal foramen in young specimen.

A cast in paraffin of the brain cavity of *M. gregorii* has been taken; also a plasticine model squeezed into the different parts in various specimens, and corrected for size from drawings of the type specimen of *M. gregorii*. Projected upon drawings of this model (figs. 46, 47) are the exact positions of the various nerve exits as they appear in the sagittal and frontal sections (figs. 25, 38, 39).

It has been noted that the brain cavity of *Sphenodon* does not closely reflect the form of the brain and is much larger than the brain. This has produced some uncertainty as to the value of interpreting so-called brain casts and molds of fossil reptiles. Examination of the alligator shows that the space between the dura mater and pia mater is slight, and the bony parts reflect fairly accurately the major subdivisions of the brain, which fills the cavity except in the posterior medullar region. The medulla is considerably smaller than the foramen—doubtless to allow for turning movements of the head. In lizards a few representative genera, at least, have similar relations between the form of the brain and the bones which closely invest it.

If the condition in *Sphenodon* actually occurs in fresh material, it differs from other reptiles and may be unique. I am inclined to believe, with Lambe, that the brain cavity of dinosaurs reflects fairly closely the form of the brain; that of phytosaurs also appears to, although not so closely as that of mammals.

The medulla doubtless did not completely fill its cavity, and the form and position of the optic lobes and cerebellum have left no definite impressions on the brain case.

In the preparation of the model, figures of which are given, it may be understood that the periphery follows the surfaces indicated by the bones. Dotted lines indicate conjectural structures which have not left recognizable traces in the bone. The solid peripheral lines probably indicate the outer surface of the dura mater. The brain itself and particularly the medulla were doubtless slightly smaller than the dimensions of the model.

The brain is of peculiar form and relatively smaller than in recent crocodilia. Its most conspicuous features are the nearly vertical position of the brain stem and the enormous size of the epiphyseal region. The olfactory tract, hypophysis, and medulla are also relatively large. There was evidently a distinct pons varolii. The cerebellar region is narrow and constricted posteriorly and the cerebrum is vertically elongated, with an anterior process projecting from each hemisphere above the olfactory lobe.

The *olfactory bulbs* are very large and elongated and each side is partly divided by a longitudinal ridge in the frontal bone. The inference might be that these two grooves in the roof of the anterior olfactory canal accommodated two divisions of the bulb which may represent a dorso-median branch of the olfactory nerve and a ventro-lateral branch. Such a division of the olfactory bulb, on each side, is present in the anuran and caecilian amphibians and certain elasmobranchs. It is also represented by double olfactory centers in the Urodela, where the external parts are not plainly separable. The bulbs are divided externally in modern crocodilians.

In the crocodile, Meek's figures (1911, figs. 7, 8) show both dorsal and ventral olfactory nerves proceeding independently from the olfactory bulb. Meek and others have demonstrated the presence of a vestigial organ of Jacobson in the crocodilian embryo, its position being in the floor of the nasal chamber, just in front of the inner (dorsal) entrance of the choanæ.

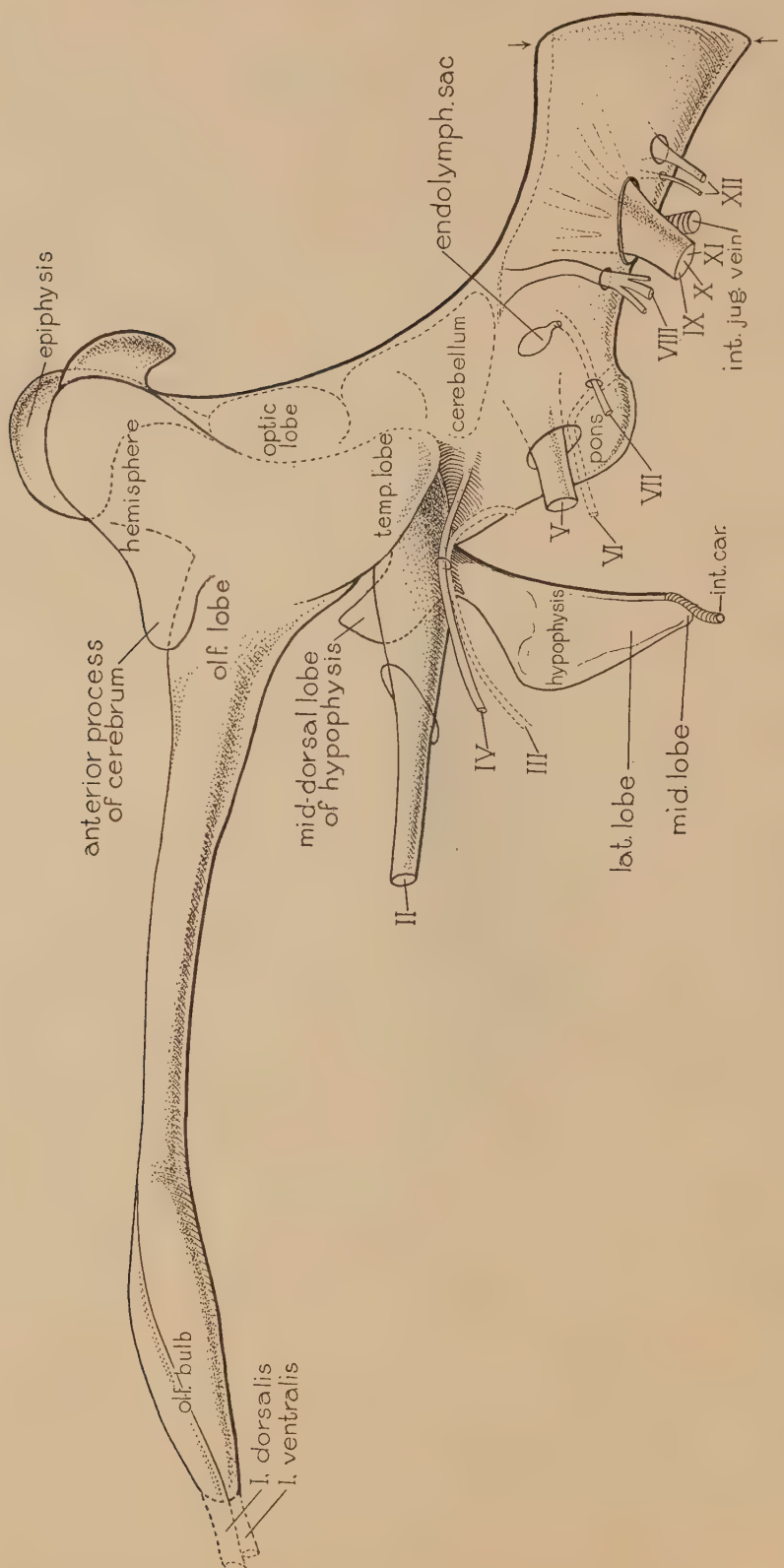

Fig. 46. The brain of *Machaeroprosopus*, drawn from a plasticine model based chiefly upon casts, measurements, and impressions of the brain case of *M. gregorii* (type), left side, X1. See also fig. 47.

According to Norris and Miss Hughes (1918), "in the Amphibian in general, the posterior ventral glomeruli (belonging to the ventro-lateral branch of the olfactory nerve) are related to Jacobson's organ, but not exclusively so. . . . . In *Dermophis* the ventral olfactory nerve supplies Jacobson's organ and the olfactory epithelium covering the convexity of the ridge on the floor of the olfactory chamber. The dorsal nerve supplies the medial, dorsal, and lateral walls. In *Herpele* the ventral nerve supplies Jacobson's organ and the epithelium of the floor; the dorsal nerve, the medial and lateral walls."

Assuming from the size and structure of the internal choanæ, that Jacobson's organ was present in phytosaurs in the usual position it would be probable that a ventral branch of the olfactory nerve passed forward and downward between the dorsal margins of the pterygoids to reach the region of Jacobson's organ and the floor of the olfactory chamber, while the dorsal branch of the olfactory nerve continued forward beneath the squared-off lower borders of the septomaxillary, followed this bone through the narial septum, and innervated the large chamber anterior to the nares. Here there are evidences of thin, plate-like, ossified, turbinal bones with deep mid-dorsal sulci between them in the septomaxillae (figs. 22, 27). These furrows and plates provided space for what must have been a considerable area of sensory, olfactory epithelium.

The *cerebrum* appears to be vertically elongated. The base of the temporal lobe is distinctly marked by a bulbous internal process of the presphenoid. A groove in the side of this process marks the course of the fourth nerve. A prominent ridge in the postero-dorsal part of the laterosphenoid indicates a constriction between the olfactory lobe and the cerebrum. Above the ridge a wide fenestra leads forward and downward into a deep cavity lying above and lateral to the postero-dorsal end of the olfactory lobes. This cavity passes between the laterosphenoid and parietal and ends in the frontal and laterosphenoid just anterior to the fronto-parietal suture. It does not continue forward as a foramen. I have thought that this cavity represented an anterior process of the cerebrum, because of its size and position well in front of the epiphysis. If it carried a process of the epiphysis, that structure must have been of extraordinary size and anterior extent.

This process is evidently what Cope (1887 and 1888) has regarded as an "orbito-pineal" process of the epiphysis in *Machaeroprosopus buceros* and in *Diadectes phaseolinus*. Case (1921) has noticed a very small process in a more dorso-lateral position in *Desmatosuchus*.

The brain cast of *Tyrannosaurus* shows a small antero-dorsal process in the cerebral region, which extended into a pit or large foramen between the laterosphenoid and parietal. This is possibly the same structure which I have just described in *Machaeroprosopus*, but the homology is by no means certain. Hay (1909) finds a large foramen at this point, in *Triceratops*, which he believes to have transmitted a blood vessel. There is no foramen here, in *Machaeroprosopus*, and no separate foramen for the fourth nerve. There may however have been such a foramen in *Tyrannosaurus*, although I do not find its exit on the outer surface of the neuro-cranial wall in Osborn's figures.

The *epiphysis* appears to have been of great size. A dome for its reception is excavated in the ventral surface of the parietals. I regard its identity as fairly certain because of the presence of a vestigial pineal pit in a young skull of *Machaeroprosopus lithodendrorum*. This pit leads toward the exact apex of the parietal vault. In larger skulls the foramen is entirely obliterated.

Behind the dome of the epiphysis are a pair of curved, conical pits extending backward and downward into the dorsal end of the supraoccipital (fig. 40). Each of these cavities is bounded dorsally by the parietal; posteriorly, ventrally, and antero-ventrally by the supraoccipital, and antero-medially by the laterosphenoid. I have been unable to determine what structures entered these post-epiphyseal pits. They may have received portions of the epiphysis, cerebral hemispheres, the velar arch, or even the paraphysis. In the embryology of the crocodilians as described by Voeltzkow (1903) and by Reese (1910), a median paraphysis is found lying in front of the post-velar arch or dorsal sac ("zerbelpolster"). The paraphysis may be slightly paired in the frogs but is single in the crocodiles and alligators. No epiphysis is recognized in the crocodilians. In other reptiles, however, the epiphysis lies behind the dorsal sac. It is therefore highly improbable that these paired structures, extending as they do behind the epiphysis in phytosaurs, represent the paraphysis.

I also think it unlikely that any part of the cerebrum would have entered these pits, situated as they are well behind the cerebral spaces and opening at an angle through the brain wall.

The presence of a foramen is suggestive of a connection with the velar apparatus, or the glandular portion of the epiphysis. From the apex of each pit a foramen passes downward and forward through the supraoccipital to emerge in the brain cavity near the center of the postero-dorsal mid-line. I have called this the velar foramen thinking that it may have conducted a vessel from or to the velar region, but it may be that it carried a vessel to the pineal gland.

A median posterior process in the post-epiphyseal region appears in Cope's (1888) cast of the brain case of *Machaeroprosopus buceros*. From its position this must be at the juncture of the pits which have just been described. But Cope has not represented the structure in its full extent, as a paired diverticulum. It is extremely significant that the brain cast of *Diplodocus* (Osborn, 1912), shows a pair of processes almost identical in form and position with this structure in phytosaurs. Also in *Tyrannosaurus*, and possibly in *Allosaurus*, a postero-dorsal process appears which is probably homologous with that found in *Diplodocus* and which has been called by Osborn a part of the epiphysis.

In *Diademodon* (Watson, 1913) there is a postero-dorsal outpocketing of the cranial roof well behind the epiphysis. Watson considers this to be above the cerebellum and in his sagittal section (fig. 5) does not project the cerebellum up into it. The position of this pocket is farther back in *Diademodon* than in the dinosaurs and phytosaurs.

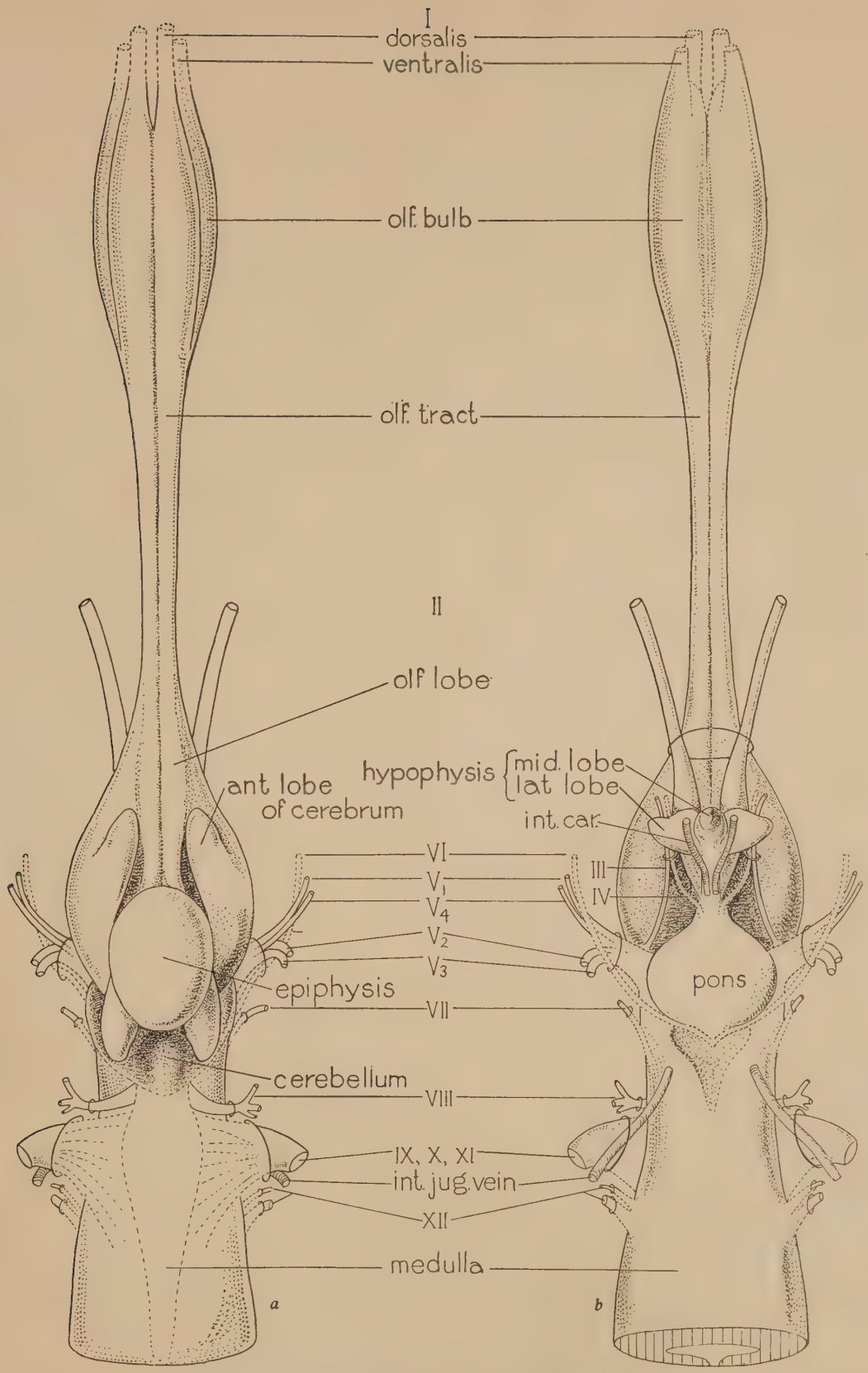

Fig. 47. Brain of *Machaeroprosopus*, ×1. *a*. Dorsal view. *b*. Ventral view.

The position, but not the size, of the *optic nerves* is marked by the horizontal optic fissure (fig. 36). In front of the brain this fissure joins the hypophyseal foramen. Within its dorsal border is a vertical mid-dorsal pit. Its floor is concave and doubtless supported an optic tract of small or moderate size. The dorsal pit (fig. 25) is puzzling. It does not communicate directly with the floor of the olfactory tract. It must therefore have received either a portion of the optic tract or of the hypophysis. The optic chiasma is not located in this dorsal position in other vertebrates. The hypophysis does not usually develop a dorsal lobe of this extent.

Gaupp (1893), however, has found a large antero-dorsal lobe in this position in the embryo of *Lacerta agilis*, and Reese (1910, figs. 4*b*, 4*c*, 5*c*) shows that in the development of the hypophysis of the American alligator, three anterior lobes are formed of which one is mid-dorsal in position and remains in connection with the main body.

It is possible then that a dorsal lobe of the hypophysis in *Machaeroprosopus* extended up in front of the optic commissure and between the optic nerves, to insert into the mid-dorsal pit above the optic tract.

On the ventral mid-line, in the suture of the conjoined laterosphenoids, and just in front of the optic fissure, is a small foramen passing from the orbit to the base of the olfactory lobes (figs. 25, 36*r*). It is not likely that this foramen carried a nerve. A nerve entering the orbit from the olfactory region is stated by Cope (1888) to occur in *Alligator*, but there is no evidence of such a structure according to one of my students, Mr. Frank Mayner, who has investigated this point. The foramen probably conducted a mid-ventral blood vessel.

The ventral portion of the *hypophysis*, descending vertically into the well marked sella turcica, is relatively large and broadened laterally somewhat as in the primitive crocodilian *Teleosaurus* (Morel de Glasville, 1876). It is relatively larger than in *Triceratops* and *Edmontosaurus* (Lambe, 1920) but possibly not so large relatively as in *Diplodocus* and *Desmatosuchus*. The great size of the hypophysis in the dinosaur has often been commented upon but the differences in size between the hypophyses of *Triceratops*, *Edmontosaurus*, and *Alligator* were certainly not great when it is remembered that a portion of the optic tract enters the region of the pedicle of the hypophysis.

Evidence for the positions of the *third* and *fourth nerves* has been previously discussed. They apparently entered a common foramen situated at the antero-dorsal extremity of the proötic in its suture with the presphenoid.

The *fifth nerve* was evidently of large size and the courses of its exterior branches are indicated by grooves in the outer neuro-cranial wall (figs. 36, 37, and 38). Its foramen lay almost entirely within the proötic but was touched inwardly by the basisphenoid and outwardly by a ridge of the laterosphenoid.

No separate foramen for the *sixth nerve* has been located. The nerve may have passed forward with the third and fourth but more probably it entered the foramen of the fifth.

The *seventh nerve* was very small and left the skull through a foramen located behind and below that of the fifth. The inner aperture lay in the suture between basioccipital and proötic; the outer, entirely in the proötic, in a narrow cleft on the side of the paroccipital process of that bone.

The floor of the brain cavity immediately below the foramena of the fifth and seventh nerves was hollowed into a smooth basin in the basisphenoid and bounded posteriorly by the conjoined lobular, anterior processes of the exoccipitals. This basin evidently received the *pons varolii* which must have been more highly differentiated than in other known reptiles. The cause of this development may be sought in the great enlargement of the jaw muscles in phytosaurs. The nerves innervating these muscles have their centers in the pons.

The course of the *eighth nerve* is indicated by a vertical groove encircling the postero-dorsal border of the capsular region (just behind the pit for the endolymphatic sac). The foramen for the acoustic nerve was apparently single and located in the suture between the proötic and paroccipital.

The foramen for the *ninth, tenth,* and *eleventh nerves,* together with the jugular vein, was large and occupied a ventral position in the suture between exoccipital and paroccipital.

The foramen for the *twelfth nerve* was double as it is in the crocodilians, and in *Trachodon, Diplodocus, Diademodon* and the marsupial *Trichosaurus.* It seems improbable that one of these foramena in the fossil reptiles transmitted a vein as Hay suggests.

The *medullar cavity* is nearly cylindrical and smaller anteriorly. The greatest width of the cavity was less than that of the cervical portion of the spinal canal.

Comparisons.—A dorsal flexure of the mid-brain occurs in the saurischian dinosaurs, *Allosaurus, Tyrannosaurus, Camarasaurus,* and *Diplodocus.* It is absent so far as known in the ornithischia. Its presence in phytosaurs (and in *Erythrosuchus?*) strengthens previous views of the relationships of the Saurischia and Phytosauria. In general the Permian reptiles and amphibians have a low, horizontal brain case. *Diopeus* however appears to be flexed dorsally, also the therapsid *Diademodon.* A flexure would appear to be present in *Diadectes* from Cope's figures, but Watson has cast doubts on the accuracy of Cope's cast. The condition is not found in the primitive crocodilians *Teleosaurus* and *Steneosaurus* nor in modern reptiles and amphibians. It reaches its greatest development among reptiles, so far as is known, in *Machaeroprosopus.*

It might be supposed that the pronounced brain flexures of phytosaurs are correlated with the mechanical advantage of the great depression of the condyle. This position of the condyle would permit of greater leverage for the dorsal cervical muscles attaching to the squamosal region, and may account for the extreme development of the flexures in phytosaurs but it does not account for similar conditions in such forms as *Diplodocus.* The brain flexures are so widely distributed as to be of some phylogenetic interest.

An enlarged epiphysis is present in *Allosaurus*, *Tyrannosaurus*, *Diadectes*, and in many primitive reptiles and amphibians. The epiphysis is absent in crocodilians, the stalk usually figured as such being the paraphysis. It is of course present, but small, in lizards. It apparently reaches a very high development in phytosaurs where it may be largely or entirely represented by an enlarged pineal gland or by the dorsal sac.

The olfactory region is large in *Allosaurus*, *Tyrannosaurus*, *Triceratops*, and *Edmontosaurus*. It is large and extremely attenuate in phytosaurs, much more so than in crocodilians where it might be expected to be longer owing to the anterior position of the nares. In the phytosaurs it is more completely enclosed in bone than in other known reptiles except possibly the cynodonts.

The internal distribution of the cranial foramina does not present any striking differences in comparison with crocodilians and dinosaurs. Separate foramina for the fourth and sixth nerves however are present in many or all of these forms. In *Desmatosuchus* there is perhaps no separate foramen for the fourth nerve but there may be one for the sixth.

Externally the cranial foramina are more similar in dinosaurs and phytosaurs than in crocodilians and phytosaurs. This is due to the enclosure of the tympanic cavities in crocodilians and the consequent rearrangement of the external openings of the foramina in those forms.

Mehl's Study of the Phytosaur Brain

Since writing the preceding account of the brain of *Machaeroprosopus*, I have received Professor M. G. Mehl's recent studies of his new genus *Pseudopalatus* (1928*a*). I have elsewhere (p. 144) noted that this genus appears to be founded upon a species very similar if not identical with *Machaeroprosopus tenuis*, and that its only important assigned character, the closure of the palate, may be due to a misinterpretation of the one side of the palate which is preserved in the type.

Mehl's study of the brain of *Pseudopalatus* brings him to radically different results than mine. His interpretations are based upon a gelatin mold of the brain case which indicates, in general, the same parts and proportions that appear in *Machaeroprosopus*. The brain flexures however are not shown, some of the nerve exits are differently located, and the chief parts receive different names.

I am not inclined to regard even these great differences as due to an actual difference in the material (which came from the same general locality) but to differences in interpretation and methods of study. The olfactory lobe of Mehl is the olfactory bulb of my figures, the location of his olfactory bulb being conjectural. He has located the "fore-brain" where I place the olfactory lobes and does not recognize the presence of distinct cerebral hemispheres. He regards the bilateral swellings, which I have called the anterior processes of the cerebrum, as the mid-brain; and the cerebellum in his figures occupies the dome of the epiphysis of mine. He does not recognize the presence of an epiphysis. The medulla of Mehl includes the cerebellum, the optic lobes, and part of the cerebrum of mine.

Mehl places the exit of the fifth nerve directly above the hypophysis, the seventh nerve of his figures is the endolymphatic sac and duct of mine, and the three roots of the sixth nerve in his cast are not shown in my restoration unless they may be represented by the partly divided fifth foramen together with the seventh. He separates the exits of the ninth and tenth nerves and omits the twelfth which appears as a distinct foramen or pair of foramina in a great number of recent and fossil reptiles. His "*lobus lineæ lateralis*" appears at the lower entrance of what I have called the velar foramen.

Mehl concludes that the endocranial mold which he has described is "quite unreptilian," and suggests its similarity to modern fishes. He believes that the differences between the brains of his phytosaur and of "dinosaurs and crocodiles bespeak a much more remote relationship between these other groups than has been suspected" and concludes that "this fish-like brain suggests a phytosaurian line of descent distinct from a time considerably before the differentiation of the reptilian groups with which it is usually classed."

My own views of the relationships of the phytosaurs as indicated by the brain, as I understand it, are offered elsewhere (pp. 151–152).[9]

TACTILE ORGANS

Scattered over the enlarged tips of the rostrum and lower jaws are the openings of funnel-shaped foramina which might at first glance be regarded as nutrient. Their structure and distribution indicate however that they probably have another or at least an additional function. They are larger on the ventral surfaces of the dentary tips and are more abundant on the extreme tips than on the sides of the dentary and premaxillary enlargements. They are larger at the surfaces of the bone than within, and they diminish in number posteriorly. There are about forty of these pits on each ramus of the dentary in a specimen of *M. adamanensis*.

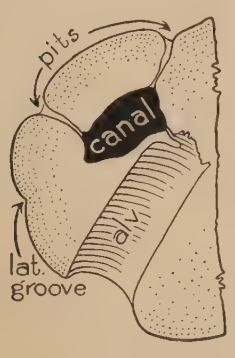

Fig. 48. Transverse section of right mandibular ramus of *M. adamanensis*, 7038/26756, at the level of the sixth anterior premaxillary alveolus, to show pits supposedly for cutaneous tactile organs, ×1½.

In cross-section it may be noted (fig. 48) that each of these pits communicates with the central canal of the dentary by a narrow foramen. In the alligator this canal carries blood vessels to the skin and teeth as well as sensory branches of nerve V_3. Also in the alligator there are regularly spaced, pigmented tubercles over the anterior and antero-ventral surfaces of the snout and lower jaws. These tubercles, as I have observed, are supplied with nerves which branch from fibers passing outward through these anterior foramina of the jaws.

[9] See also E. C. Case's recent paper (*Jour. Comp. Neur.*, vol. 45, 1928, pp. 161–168) on an endocranial cast of a phytosaur from Texas. Case regards the foramen which I have called the "velar" foramen as nutrient. He identifies two separate apertures for the sixth nerve near the hypophyseal fenestra and in front of the pons. He unites the inner portion of the foramen for the seventh nerve with the eighth. He regards the twelfth nerve as having a single exit, and he gives an excellent description of the inner ear.

No careful study has yet been given to the nerve endings, but it is probable that they are touch receptors transmitting stimuli from regions of the head which are concealed from the lines of vision.

The anterior parts of the jaws in the phytosaurs are not within the field of vision and highly developed tactile structures at the tips of the jaws would obviously be of service.

CLASSIFICATION OF THE PHYTOSAURS

HISTORY OF THE CLASSIFICATION

The reptilian group Parasuchia was established by Huxley (1875) as a suborder to include the phytosauroid genus *Stagonolepis* and the phytosaur *"Belodon."* Huene (1902) recognizing the affinity of the aëtosaurs includes them in the Parasuchia. McGregor (1906) adopts this view and raises the Parasuchia to ordinal rank above the suborders Aëtosauria and Phytosauria. Huene (1911) in a subsequent revision, made after a study of Jaeckel's genus *Mesorhinus*, regards the Parasuchia as a "sterile sidebranch" of the Pseudosuchia including only the families Stagonolepidæ (genera *Mesorhinus* and *Stagonolepis*) and the Phytosauridæ (genera *Rileya*, *Parasuchus*, *Paleorhinus*, *Phytosaurus*, and *Mystriosuchus*). In his last statement Huene (1922*a*) reestablishes the old reptilian order, Thecodontia of Owen to include the Pelycosimia, the Pseudosuchia, and the Parasuchia. In this third suborder he places the Desmatosuchidæ, the Stagonolepidæ (with the genera *Mesorhinus*, *Stagonolepis*, and *Stegomus*) the Phytosauridæ, and the Mystriosuchidæ.

Opinions differ as to what constitutes the natural subdivisions of the phytosaurs—omitting from this category the Desmatosuchidæ and Stagonolepidæ. McGregor (1906) suggests that the forms with heavy, crested snouts and the more slender-snouted forms are parallel, independent developments in the Old World and the New. Huene (1911) recognized fundamental differences between the genera *Mystriosuchus* and *Phytosaurus*, especially in the nature of the dermal scutes and (1913) in the shape of the cervical and dorsal vertebræ, the interclavicle, the ilium, and the femur. He believed (1913) that the American *Rutiodon* and the European *Mystriosuchus* should probably be united in one genus. He afterwards (1915) referred Cope's *"Belodon" buceros* to the genus *Phytosaurus*, following restudy of Cope's type skull. At this time Huene established the family Mystriosuchidæ including all the phytosaurid genera except *Phytosaurus* which he regarded as the sole member of McGregor's Phytosauridæ, *sensu strictu*. Characters of the Mystriosuchidæ which Huene gave at this time were: "a broad infratemporal fenestra and a relatively great supratemporal fenestra, cutting further into the parietal roof; in the body . . . . subquadrate and scale-like dermal scutes."

Case (1922, p. 55) states that:

"a review of the known skulls of the Parasuchia reveals the fact that they may be divided into two more or less clearly marked groups—those with long, slender, depressed rostra and those with elevated rostra. To the first group, the Mystriosuchid group, belong *Mystriosuchus*, *Rhytidiodon*, *Paleorhinus*, and *Promystriosuchus;* to the second group belongs *Phytosaurus* . . . . . Inter-

mediate between the two are the forms which have been described by Cope as *Belodon buceros* and by Mehl as *Machæroprosopus validus*. In the opinion of some workers, *Belodon buceros* Cope and *Machæroprosopus validus* Mehl should be placed in the genus *Phytosaurus*. The two specimens described in this volume as *Leptosuchus* help to further bridge over the gap between the two groups."

A number of interesting suggestions regarding the classification of the phytosaurs have been offered by Abel (1922). Abel believes that *Phytosaurus kapffi* is the male and *Mystriosuchus planirostris* and *plieningeri* are females of the *same species;* that *Machaeroprosopus buceros* and *M. validus* are synonymous and represent the male of the species of which *Rutiodon carolinensis* is the female; and that the European *Phytosaurus* and the American *Machaeroprosopus* and *Rutiodon* represent two species of the same genus.

Abel reaches these conclusions after an extensive study of the tumor pockets on the dorsal borders of various phytosaur skulls. He believes that these abscesses were due to bite wounds received during fights among the males, and more rarely among the females; that the swollen-snouted forms reflect the results of these injuries and are consequently the males, while the slender-snouted forms, which show fewer abscesses, are the females. He draws some parallels from modern reptiles, cetaceans, and other forms and recognizes the extreme differences reported to be found in the dermal scutes and skeleton of the long- and the short-snouted European phytosaurs.

I fully agree with Abel's idea that the abscess or tumor pits frequently found on the phytosaur rostrum are the results of wounds received in combat (in fact I had independently reached the same conclusion), but I cannot subscribe to his systematic views for the following reasons:

(1) Slender- and heavy-snouted forms are not found together in every horizon where, if they represented males and females, they should be expected. No heavy-snouted individuals have been found in the lower horizons of the Lower Chinle.

(2) No forms that could be regarded as *Rutiodon* have been found in western North America where, if they represented the females of *Machaeroprosopus validus* and *buceros*, they should certainly be expected. In fact there is some reason to regard the type specimen of *M. validus* as a female rather than a male.

(3) Both slender- and heavy-crested forms in western North America are known to have possessed a similar type of dorsal armor resembling that of *Mystriosuchus* and *Rutiodon*. Plates similar to those of *Phytosaurus* are but rarely found and indications are that these plates accompany an animal having a skull and skeleton somewhat different from *Machaeroprosopus*. These differences in the dermal armature of the European forms have led Huene to regard them as distinct families. Abel treats them as sexual differences in the same species! Each view is perhaps too extreme.

(4) A separation between males and females in *Machaeroprosopus* can be made on other grounds than the differences in the rostral crests. An elevation of the borders of the nares, as previously outlined, is present in about half of the known forms. In some species those adult individuals having crater-like nares possess

more slender rostra than those in which the nares are depressed, but these differences are by no means so pronounced as Abel's theory would require, and are not reflected in the skeleton and dermal scutes.

(5) Nothing like the extreme sexual dimorphism, which Abel postulates for phytosaurs, is known in crocodilians or in any other reptiles, living or fossil.

(6) There are a number of differences between *Rutiodon* and *Machaeroprosopus* and between *Machaeroprosopus* and *Phytosaurus* to which I should give far more weight than does Abel (cf. p. 90).

So far as I know, Huene (1922*a*, *b*) still maintains the following views of the classification of the Parasuchia:

Fam. *Desmatosuchidae* Case 1920	*Desmatosuchus*
Fam. *Stagonolepidae* Huene 1912	*Mesorhinus*
	Stagonolepis
	? *Stegomus* (*arcuatus*)
Fam. *Phytosauridae* McGregor 1906	*Phytosaurus*
Fam. *Mystriosuchidae* Huene 1915	*Angistorhinus*
	Paleorhinus
	Machaeroprosopus
	Rutiodon
	? *Episcoposaurus*
	? *Parasuchus*
	? *Rileya*
	Angistorhinopsis
	Mystriosuchus

A note is added that "the systematic position of the singular genus *Typothorax* [cf. Huene, 1915] is not yet entirely certain."

The question of the relationships of the European to the American heavy-snouted phytosaurs hinges partly upon the character of the dermal scutes. If the dorsal armature ascribed to *Phytosaurus kapffi* is really known to be associated with typical skull material of that genus there can be little question of the generic distinctness of that form. The Arizona phytosaurs described in this paper, despite certain skull resemblances to European genera, are, by reason of their skeletal differences, assigned to the well defined American genus *Machaeroprosopus* Mehl.

Huene in his later work (1926) recognizes the American genera as distinct from similar European forms. I concur in this. The American phytosaurs seem to appear in association with earlier faunas than the European forms and, with the exception of the European *Mesorhinus*, are more primitive. They undergo some radiation with the development of many varied species, before the more highly specialized genera appear in Europe.

I am able to present sufficient evidence from our collections to support Huene's view that the Arizona phytosaurs, of which good skull material is now known, have closer skeletal resemblances to *Mystriosuchus* than to *Phytosaurus*. Also, the extreme posterior position of the external nares (behind the choanæ) should identify *Machaeroprosopus* as a distinct genus.

The genera based upon skulls described during the past thirty years seem fairly well established. But they will be properly located in the system only when skeletal material is discovered, particularly the dermal scutes, vertebræ, and girdles. It is noteworthy that the dermal scutes may differ greatly in phytosaurs without any profound differences in skull structure. This makes it regrettable that so few American skulls have been accompanied by skeletal material.[10]

The form of the rostrum is insufficient in itself to furnish a basis for a major classification. It seems that in the Angistorhininæ there is a tendency for the skull and rostrum to become compressed, in the Phytosaurinæ to be depressed. Both methods perhaps serve to gain additional supporting strength for the base of the heavy snout. The method usually employed is to increase the height rather than to increase the width and flatness.

NOMENCLATURE

Von Meyer's original description (1842) of his new genus and species *Belodon plieningeri* is as follows: "ein saurus mit gewohnlicherer Zahnstruktur, dem ich wegen der Pfeil-formigen Gestalt seiner Zähne den Namen Belodon Plieningeri gegeben habe." This does not distinguish the species, much less the genus, from *Phytosaurus kapffi*. The original type material, so stated, was described and figured by von Meyer in 1844 (p. 44, pl. 12, figs. 20, 21), yet here, while the description is complete, the material is inadequate to identify the form and does not establish the species as valid. At a much later period von Meyer (1861) was still in great doubt as to specific differences in the European phytosaurs and merely suggested, on the basis of much new material, that the smaller and more slender form was *B. plieningeri* and the larger, crested form was *B. kapffi*. The latter he regarded as synonymous with *Phytosaurus cylindricodon* and *cubicodon*. In 1863 he adds a third species, *planirostris*, and in 1865 after the finding of complete skulls of each kind he regards his three species as well established.

This leaves the proper assignment of the type material of *B. plieningeri* in doubt and the usual procedure would be to restrict the generic and specific names to the type specimen. No other name being available a new one would have to be applied to the material subsequently referred to *plieningeri*. The generic name for the better known material would automatically become *Mystriosuchus*, which is the next available generic name.

Huene (1922*a*) objects to the use of *Belodon* simply on account of the confusion that might be entailed and adopts the use of *Mystriosuchus*, but it seems plain that the name *Belodon*, under the rules of nomenclature, should be restricted to the type material.

[10] Mehl (1928*c*) has described the dermal scutes of *Paleorhinus* as being subcircular, but does not indicate whether or not these are mid-dorsal scutes.

I shall not meddle with the well established name *plieningeri*, preferring to let von Meyer's subsequent designation of his specimens fix the specific but not the generic name of this now well-known form. This is "inconsistent" but is surely "in the interests of stability."

I see good reason for separating the Pennsylvania and New Jersey phytosaurs from the North Carolina form *Rutiodon*, and have therefore resurrected the genus *Clepsysaurus* as separate from *Rutiodon*. *Clepsysaurus* may prove to be identical with *Machaeroprosopus*, but lack of skull material of the eastern form prevents a definite statement. There appear to be no good grounds at present for the recognition of any other eastern genera. Those described on teeth are very questionable.

A summary of the present state of the nomenclature, including my own views, is expressed in the following list, where I recognize as distinct those genera in boldface and the species treated as "referred." The "synonyms" include names which are not considered tenable.

Revised List of Genera and Species of Phytosauridae

Phytosaurus Jæger, 1828, p. 22, pl. 6

Type.—*P. cylindricodon, idem;* based on the symphyseal portion of a mandible with alveolar casts which were mistaken for the crowns of teeth.

Type locality.—"Der Steinbruch . . . . zwei Stunden von Tübingen nahe bei altenburg oder Rübgarten am nördlichen Ufer des Neckars, an einem Hügel auf welchem einst die Burg Wildenau stand." (? Upper Keuper, in a formation similar to the Stubensandstein.)

Referred.—*Belodon Kapffi* H. von Meyer, 1861, pp. 256, 271–315, pls. 28, 30–43; based on skulls. Type locality: Upper Keuper (Stubensandstein) in the valley of Stuttgart. Huene (1911, p. 36) regards *kapffi* and *cylindricodon* as synonymous but retains the former name because of the unsatisfactory state of the type material of *cylindricodon*.

Synonyms.—"*Nicrosaurus* O. Fraas, 1866, p. 210." Type, *Belodon kapffi* H. von Meyer (*ante*). A substitute name ? (*vide* Abel, 1922, p. 37).

Lophoprosopus Mehl, 1915, p. 163. Type, *Belodon kapffi* H. von Meyer (*ante*). A substitute name. Establishment of the generic identity of *Phytosaurus cylindricodon* and *Phytosaurus kapffi* renders the generic name *Phytosaurus* again available for *kapffi*.

? *Zanclodon arenaceus* E. Fraas, 1896, p. 18; based on a fragment of a mandible. Type locality: "Schilfsandstein der Feuerbacher Haide," near Stuttgart (Lower Keuper). This species has been referred to *Phytosaurus kapffi* (cf. McGregor 1906).

Mystriosuchus E. Fraas, 1896, pp. 16–17, pl. 5

Type.—*Belodon planirostris* H. von Meyer, 1863, pp. 241–243, pls. 41, 42; based on a skull. Type locality: ? "im Stubensandstein eröffneten Steinbrüche zur Germarkung Aixheim [Stuttgart] gehören," Upper Keuper.

Referred.—*Belodon Plieningeri* H. von Meyer, 1842, p. 302; based on a fragment of a jaw and teeth (cf. von Meyer and Plieninger, 1844, p. 44, pl. 12, figs. 20, 21). Type locality: "Dem Stubensandstein der Keuper-Formation von Löwenstein in Württemberg" (Upper Keuper). An inadequate description. The specific name may be regarded as fixed by von Meyer's later descriptions of the material (1861 and 1865). Huene (1922*a*, p. 146) considers the species as generically referable to *Mystriosuchus*.

SYNONYMS.—? *Termatosaurus* H. von Meyer and Plieninger, 1844, p. 123, pl. 12. Type: *T. Albertii, idem;* based on isolated teeth. Type locality: "Rhaetic" of Württemberg. This genus is referred by E. Fraas (1896, p. 17) to *Mystriosuchus.*

? *Belodon ingens* E Fraas, 1896, p. 15; based on an unprepared skull in which Fraas sees "zwar viel Aehnlichkeit mit B. Kapffii." Type locality: "Stubensandstein von Aixheim bei Spaichingen." Huene (1922*a*, p. 146) regards it as probably synonymous with *B. plieningeri.*

Parasuchus Huxley, 1870, p. 49 (*nomen nudum*; first description by Lydekker, 1885, pp. 22–25, pl. 3).

TYPE.—P. hislopi, Huxley (MS) in Lydekker *loc. cit.;* based on skull fragments.

TYPE LOCALITY.—Maleri, India; from the Maleri Triassic beds in the Gondwana formation.

Clepsysaurus Lea, 1851*b*, p. 205

TYPE.—[sp.] *Pennsylvanicus*, Lea, 1851*a*, p. 172; based on vertebræ, ribs, and teeth (cf. also Lea, 1852, 1853).

TYPE LOCALITY.—Upper Milford, Lehigh County, Pennsylvania, "on Hoosac's Creek, a tributary of the Perkiomen."

REFERRED.—*Rutiodon manhattanensis* Huene 1913, p. 277, fig. 14, pl. 50; based on parts of skeleton in the pelvic region. Type locality: "near Fort Lee on the right side of the Hudson River opposite New York (City) . . . . 20 feet below the thick sheet of basalt of the Palisades," at the base of the Newark Triassic. While this species may be synonymous with *pennsylvanicus* it is a fairly well established form and it is consequently desirable to retain it until such identity be proven.

SYNONYMS.—*Centemodon* Lea, 1856, p. 78. Type, *C. sulcatus, idem;* based on a tooth. Type locality: in dark shales of the "Red sandstone formation . . . . on the Schuylkill" River near Phoenixville, Pennsylvania.

Eurydorus Leidy, 1859, p. 110. Type, *E. serridens, idem;* based on isolated teeth. Type locality: vicinity of Phoenixville, Chester County, Pennsylvania, in shales from "the railway tunnel."

Belodon lepturus Cope 1870, pp. 59–61, pl. 14; based on vertebræ and other skeletal parts. Type locality: "bone bed in the [Reading railroad] tunnel at Phoenixville, Pennsylvania."

Clepsysaurus veatleianus Cope, 1877*a*, p. 184; based on "a single large tooth." Type locality: "Triassic of Pennsylvania," collected presumably in C. M. Wheatley's copper pyrites mines.

Palæoctonus Cope, 1877*a*, p. 182. Type, *P. appalachianus, idem;* based on "two teeth." Type locality: "found by . . . . Charles M. Wheatley, A. M., in one of his copper pyrites mines," in Pennsylvania.

Palæoctonus aulacodus Cope, 1877*a*, p. 184; based on "but one tooth." Type locality: in the Wheatley collection, presumably from his copper pyrites mines in Pennsylvania.

Suchoprion Cope, 1877*a*, p. 185. Type, *S. cyphodon, idem;* based on teeth. Type locality: presumably Pennsylvania with Wheatley collection.

Suchoprion sulcidens Cope, 1878, p. 58; (*nomen nudum;* type fixed by Huene, 1921, p. 564, fig. 5, on a tooth in the Cope collection from Phoenixville, Pennsylvania).

? *Belodon validus* Marsh, 1893, p. 170; (*nomen nudum;* type fixed by Lull, 1915, pp. 109–113, fig. 12, on a scapular fragment, Marsh's original specimen, from "Simsbury, Conn., in the quarry of Orestes Wilcox, half a mile southeast of the station. . . . . Below the anterior trap sheet, approximately the same level as *Stegomus arcuatus,*" at the base of the Newark Triassic).

All the various forms of phytosaur teeth from the Phoenixville tunnel are presumably of the same species which if distinct from *pennsylvanicus* should be called *serridens. Clepsysaurus* was evidently similar to *Machaeroprosopus* in its heterodont dentition.

Rutiodon Emmons, 1856, p. 302

TYPE.—*R. carolinensis, idem,* p. 307; based on teeth and parts of skeleton. Emmons later (1860, p. 175) describes and figures a skull, presumably of this species.

TYPE LOCALITY.—Triassic coal measures of the Deep River region near Farmville, North Carolina.

SYNONYMS.—*Rhytidodon* (*emend.*, Cope); *Rhytidiodon*, and *Rhytiodin* (*lapsi*).

Compsosaurus Leidy, 1856*a*, p. 165. Type, *C. priscus, idem;* based on four teeth. Type locality: "coal fields of Chatham county, North Carolina."

Omosaurus Leidy, 1856*b*, p. 256. Type, *O. perplexus, idem;* based on vertebræ, teeth and a dermal plate. Type locality: "coal fields of Chatham County, North Carolina."

Clepsysaurus leaii Emmons, 1856, p. 313; based on vertebræ. Type locality: in black slate formation near bridge over Smith's river, vicinity of Leaksville, North Carolina.

Rhytidodon rostratus Marsh, 1896, p. 61, fig. 2; based on a skull. Type locality: Egypt, North Carolina (so stated by McGregor, 1906).

Typothorax Cope, 1875, p. 265

TYPE.—*T. coccinarum, idem;* based on a fragment of a mandible, dermal plates and part of a vertebra (cf. Cope, 1877*b*, pl. 22; and Huene, 1915).

TYPE LOCALITY.—Triassic of the Rocky Mountains in latitude 36°, northern New Mexico. Subsequent reference (Cope, 1877*b*, pp. 8–9) indicates that the type locality is in the Triassic shales at Cerro Blanco, near Gallina in Rio Arriba County, New Mexico. Material collected by us in that region in 1928 includes four skulls probably but not definitely associated with the characteristic dermal plates of this genus. These apparently show that *Typothorax* is a true longirostral phytosaur.

Heterodontosuchus Lucas, 1898, p. 399

TYPE.—*H. ganei, idem;* based on a fragment of a mandible.

TYPE LOCALITY.—(Cf. Cross, 1908) "Clay Hill divide, 20 miles east of the north end of Glen Canyon," of the Colorado River in Utah.

Paleorhinus Williston, 1904, p. 696, fig. 6

TYPE.—*P. bransoni, idem;* based on a skull.

TYPE LOCALITY.—About 600 feet above the base of the Popo Agie Triassic beds near Lander, Wyoming. (See also Lees, 1907.)

REFERRED.—*Paleorhinus parvus* Mehl 1928*b*, p. 142, figs. 1, 2; based on portions of a skull and skeleton. Type locality: "Sage Creek Quarry," 35 miles northwest of Lander, Wyoming, in the "Popo Agie beds of the Chugwater, Triassic."

Angistorhinus Mehl, 1913, p. 186

TYPE.—*A. grandis, idem;* based on a skull.

TYPE LOCALITY.—"Triassic of Wyoming along the Popo Agie River." (See also Mehl, 1915.)

REFERRED.—*Angistorhinus maximus* Mehl, 1928*b*, p. 158, figs. 3–6; based on posterior parts of a skull and mandible. Type locality: "Popo Agie beds of the Chugwater Triassic, about 15 miles south of Lander, Fremont County, Wyoming."

Machaeroprosopus Mehl, 1916, p. 5, figs. 1–9

TYPE.—*M. validus, idem;* based on a skull. The use of the name *validus* is unfortunate because of its prior employment by Marsh for a phytosaur of uncertain generic position.

TYPE LOCALITY.—"two miles east of Tanner's Crossing, Little Colorado River, Arizona and perhaps two hundred feet above the Lithodendron member of the Shinarump group of the Triassic," in the lower part of the Chinle Triassic.

REFERRED.—? *Belodon buceros* Cope, 1881, p. 922 based on a skull. Type locality: New Mexico. (See also Huene, 1915).

?Paleorhinus? sp. Toepelmann *in* Mehl, 1916, pp. 40–44, figs. 15–16; based on the anterior portion of a skull. Type locality: "about three-quarters of a mile northeast of Fort Wingate," New Mexico, in "red conglomeratic shales of the Upper Triassic." This perhaps represents an unnamed species of *Machaeroprosopus* in which the septomaxillaries extend forward to the point of the rostral crest.

Machaeroprosopus andersoni Mehl, 1922, pp. 144–155, figs. 1–3; based on a skull. Type locality: not definitely known, but "Triassic of Guadaloupe County, near Santa Rosa, New Mexico."

Pseudopalatus pristinus Mehl, 1928*a*, p. 7, figs. 1–7, pls. 1–3; based upon a skull. Type locality: "red clays of the Chinle formation (Triassic), about seven miles northeast of Adamana, Arizona."

Machaeroprosopus adamanensis, gregorii, lithodendrorum, tenuis, and *zunii* Camp.

Synonyms.—*?Belodon scolopax* Cope, 1881, p. 922; based on the anterior portion of a skull. Type locality: New Mexico. Possibly the young of "*B. buceros.*"

Metarhinus O. Jaekel, 1910, p. 220. Type, *Belodon buceros* Cope (*ante*). Name preoccupied by *Metarhinus* H. F. Osborn (cf. Mehl, 1916, p. 23).

Angistorhinus? sp. Mehl, 1916, p. 26, fig. 11; based on a mandible from 2 miles east of Tanner Crossing, Little Colorado River, Arizona. This is probably a young specimen of *M. validus.*

Machaeroprosopus gracilis Case, 1920*a*, p. 535 (*nomen nudum?*).

Pseudopalatus Mehl, 1928*a*, p. 7. Type, *P. pristinus* Mehl (*ante*). Mehl describes this genus as having a closed secondary palate. All other features would indicate that it is identical with *Machaeroprosopus.* If the presence of a closed palate were definitely established the genus would surely stand. However, the material includes only the left palatine and pterygoid and the evidence for union of the palatines ventral to the choanæ rests upon Mehl's observation that "the inner edge of the left [palatine] shows clearly that the pair united at the median line for about the anterior two-thirds of the length." The cross-section given in Mehl's figure 3C shows that the palatine is like that of *Machaeroprosopus.* In *Machaeroprosopus* skulls at hand it is found that a slight crushing often throws the inner edge of the palatine over to or beyond the mid-line. Such a condition would be deceptive if only one side were present and since our abundant collections from the Adamana region disclose no forms with the palatal characters of "*Pseudopalatus*" I think it safer to await better evidence before considering this genus to be established.

While it appears probable that the species *pristinus* is identical with *M. tenuis,* described in the present paper, I continue to refer my material to *tenuis* not merely on account of absence of exact data as to the stratigraphic level of *pristinus,* but because of minor differences which may be considered as specific.

Promystriosuchus Case, 1922, p. 49, pl. 11

Type.—*P. ehlersi, idem;* based on a skull.

Type locality.—"Near the head of Holmes Creek, Crosby County, Texas," in the Dockum Triassic.

Leptosuchus Case, 1922, p. 61, fig. 25

Type.—*L. crosbiensis, idem;* based on a skull.

Type locality.—"Crosby County, Texas," in the Dockum Triassic.

Synonym.—*L. imperfecta* Case, *ibid.*, p. 68; based on a skull from the "Dockum beds of western Texas." Perhaps an old adult of *crosbiensis.*

Angistorhinopsis Huene, 1922**a**, pp. 115, 145

Type.—*Mystriosuchus Rütimeyeri* Huene, 1911, p. 31, fig. 22, pls. 5(16)-7(19); based on fragments of skull and skeleton.

Type locality.—"obersten Keuper resp. Rhät. des Ergolzufers von Niederschonthal bei Liestal unweit Basel."

Rileya Huene 1902, p. 62, figs. 75, 76

TYPE.—*R. bristolensis, idem;* based on a humerus and two caudal vertebræ. This species has been considered synonymous with *R. platyodon* (Riley and Stutchbury, 1840) by Huene (1908*b* and 1911). If this proves to be the case *platyodon* becomes the type of the genus.

TYPE LOCALITY.—Quarry in the Magnesian Conglomerate "at Redland, the southeastern extremity of Durdham Downs, near Bristol," England (Middle to Upper Triassic [cf. Riley and Stutchbury, 1846, p. 349]).

REFERRED.—*Paleosaurus platyodon* Riley and Stutchbury, 1840, p. 353, pl. 29, fig. 5; based on a posterior tooth. Type locality: as given above.

The genus *Paleosaurus* (type species *P. cylindrodon*) Riley and Stutchbury, is preoccupied by *Palæosaurus* Geoffroy, 1831 (cf. Hay, 1902, p. 492). *P. cylindrodon* has, however, been referred to the earlier genus *Thecodontosaurus* Riley and Stutchbury 1838 (cf. Huene 1908*a*, p. 99). *Rileya* Huene, should not therefore be considered as a substitute name for *Paleosaurus* of Riley and Stutchbury.

SYNONYMS.—*Palaeosaurus? Stricklandi* Davis, 1881, p. 414, pl. 22, fig. 6; based on a posterior tooth. Type locality: "bone bed at Aust near Bristol," England (Middle to Upper Triassic).

Rileya stutchburi Huene, 1920, p. 144, fig. 2. Type, apparently the same humerus upon which the species *bristolensis* (*ante*) was based. Perhaps *stutchburi* has been substituted for *bristolensis* in some paper unknown to me. The other phytosaur humerus described in this paper (Huene, 1920) differs from other known phytosaurs but is not named. It comes "aus dem obern Muschelkalk von Bayreuth."[11]

FORMS OF UNCERTAIN STATUS

"*Belodon*, sp." Lydekker, 1885, pp. 21–22, pl. 3, figs. 2, 2*a*, 2*b;* comprises a conjoined basioccipital and basisphenoid from "Tiki in South Rewah," British India. Huene (1911, p. 41) refers this specimen to *Phytosaurus* with the remark that it is "nicht zu irgendwelchen Schlüssen verwerten lassen."

"*Belodon superciliosus*" Cope, 1893, pp. 12–14, pl. 1; based on fragments of a skull and a few skeletal parts. Dermal plates subquadrate. Type locality: Dockum Triassic of Texas, "in a light gray bed not far from the red bed which contained the remains of the typical specimens of *Episcoposaurus haplocerus*."

"*Palæoctonus orthodon*" Cope, *ibid.*, pp. 15–16, pl. 2, figs. 1, 1*a*, 1*b*, 1*c;* based on "a single anterior tooth of large size." Type locality: Paladuro Canyon in the Dockum Triassic of northwestern Texas.

"*Palæoctonus dumblianus*" Cope, *ibid.*, pp. 16–17, pl. 2, figs. 4, 4*a*, 4*b*, 4*c*, 5, 5*a*, 5*c*, 6, 6*a*, 6*c;* based on "numerous teeth." Type locality: same as *P. orthodon.*

The types of the above three species were deposited in the Museum of the University of Texas (Montgomery, 1904).

"*Phytosaurus* (*Machaeroprosopus*) *doughtyi*" Case, 1920*a*, pp. 529–535, figs. 5, 6; based on a portion of a skull, in the American Museum, collected and presented by Mr. George D. Doughty of Post, Texas. Type locality: Dockum beds of Texas.

It is possible that *superciliosus, orthodon, dumblianus,* and *doughtyi* represent one or more species of a genus close to *Machaeroprosopus.*

[11] To this list should be added *Brachysuchus megalodon* Case (*Mem. Univ. Mich. Mus.*, vol. 2, 1929, p. 1), a new genus and species of phytosaur from the Dockum Triassic beds "near Otischalk in Howard County, Texas, about twenty miles southeast of Big Springs." The type material consists of a well preserved skull, apparently somewhat flattened by crushing.

ARTIFICIAL KEY TO GENERA OF PHYTOSAURUS

The following is my present view of the classification of the better known genera. The key is given as an outline and omits many characters that have been previously discussed.

Parasuchians with elongate lacertiform bodies, with at least dorsal dermal plates and elongate premaxillaries.

Suborder PHYTOSAURIA

A. Dermal armor with sharp spines along sides of back.

Family DESMATOSUCHIDÆ

AA. Dermal armor without sharp spines.

I. Dermal armor complete across belly.

Family STAGONOLEPIDÆ

II. No dermal scutes on belly.

Family PHYTOSAURIDÆ

a. Nares subcircular, orbits directed upward more than outward.

Subfamily ANGISTORHININÆ

1. Supratemporal fenestræ with elevated posterior borders.

(*b*) Skull depressed, rostrum attenuate, dentition homodont. *Promystriosuchus*

(*bb*) Skull elevated, rostrum stouter, dentition heterodont. *Angistorhinus*

2. Supratemporal fenestræ with depressed posterior borders. *Angistorhinopsis*

aa. Nares compressed, orbits directed outward as much or more than upward.

Subfamily PHYTOSAURINÆ

3. Supratemporal fenestræ but slightly depressed, auditory meatus a fenestra, nares anterior to antorbital fenestra. *Palaeorhinus*

4. Supratemporal fenestræ but slightly depressed, auditory meatus a notch, nares posterior. *Brachysuchus*

5. Supratemporal fenestræ greatly depressed, auditory meatus a notch.

(*c*) Nares anterior, scutes(?). *Leptosuchus*

(*cc*) Nares posterior, scutes oval or triangular without flange.

(6) A breast shield of small scutes, limbs short, feet long, caudal spines elongate. *Mystriosuchus*

(7) No breast shield, limbs long, feet short, caudal spines short.

(*x*) Dentition homodont, rostrum attenuate. *Rutiodon*

(*y*) Dentition heterodont, rostrum shorter.

(†) Pubic articular surface of ilium shorter than ischial, fourth femoral trochanter short.

Clepsysaurus

(††) Pubic articular surface equal to ischial, fourth femoral trochanter elongate.

Machaeroprosopus

(*ccc*) Nares posterior, scutes rectangular with flange(?). *Phytosaurus*

(*cccc*) Nares posterior, mid-dorsal scutes greatly elongated, with a rounded longitudinal, ventral, thickening and with a flange. *Typothorax*

Reduced to synopsis the classification would be:

Suborder PHYTOSAURIA
- Family Desmatosuchidæ
  - Genera *Desmatosuchus*, and (?) *Episcoposaurus*
- Family Stagonolepidæ
  - Genera *Stagonolepis* and (?) *Mesorhinus*.
- Family Phytosauridæ
  - Subfamily Angistorhininæ.
    - Genera *Promystriosuchus, Angistorhinus, Angistorhinopsis*.
  - Subfamily Phytosaurinæ
    - Genera *Paleorhinus, Brachysuchus, Leptosuchus, Mystriosuchus, Rutiodon, Parasuchus, Clepsysaurus, Machaeroprosopus, Phytosaurus, Typothorax*, (?) *Rileya*.

PHYLOGENY OF THE PHYTOSAURIDÆ

In table 6 may be found the distribution of certain supposedly primitive characters of phytosaurs, most of which are regarded as paleotelic because of their occurrence in *Mesorhinus* and in other reptiles which appear earlier than the phytosaurs.

It is found that a preponderance of primitive characters (greatest *paleotelic weight*) is found in the Texas phytosaurid genus *Promystriosuchus* Case. This has thirteen of the seventeen supposedly primitive characters of *Mesorhinus*, which I have listed. *Angistorhinus* Mehl, from the Popo Agie Triassic of Wyoming, retains eleven of these characters and *Paleorhinus* Lees, from the same beds, has seven. *Angistorhinopsis* Huene, from the European Rhaetic, and *Brachysuchus* Case, from Texas, also appear to be primitive, with eight of these characters. *Leptosuchus* Case, of the Texas Dockum has five, *Rutiodon* and *Mystriosuchus*, three or four each, and *Phytosaurus* and *Machaeroprosopus* only two. Neither of these two characters, it may be stated, is of great importance since the length of the rostrum fluctuates and the presence of an otic notch rather than a fenestra is characteristic of all but one of the known forms.

It is quite evident therefore that derivation of any of the primitive forms from genera similar to the first five in the table would be exceedingly improbable.

The characters of the nares, and the greater extent of the interpterygoid vacuity seems to separate the group *Promystriosuchus, Angistorhinus,* and *Angistorhinopsis* from other phytosaurs. The dorsal position and upward, or forward and upward aspect of the orbits is another character held in common by these forms. The absence of crested species and the absence of species with a mid-premaxillary hump among these genera may also be significant. The primitive condition of the supratemporal fenestra, the interpterygoid vacuity and palatal vault is certainly so.

TABLE 6

Machaeroprosopus	*Phytosaurus*	*Mystriosuchus*	*Rutiodon*	*Leptosuchus*	*Brachysuchus*	*Paleorhinus*	*Angistorhinopsis*	*Angistorhinus*	*Promystriosuchus*	*Mesorhinus*	*Note:* A diagonal \ denotes that the character in question is intermediate or not developed so markedly as in the case of genera marked with ×.
					/	\		×	×	×	Supratemporal fenestræ normal.
					?		×	×	×	×	Eyes directed upward.
							×	×	×	×	Nares subcircular.
					\		×	×	×	?	Narial septum thin.
				\		×		×	×	×	Nares anterior.
		×	×		×	×	×	×	×	×	Squamosal short.
					×	×	\	×	×	×	Palatal vault wide.
							\	\	×	×	Interpterygoid vacuity relatively long.
×	×			\	×	×		×		?	Rostrum not exceptionally long.
		/	/						×	×	Dentition homodont.
		×	×	×	×	×	×	×	×	×	No enlarged rostral crests.
		×	?	×		×	?		×	×	Posttemporal openings small or absent.
In young										×	Pineal foramen present.
					×		×	\		×	Post-palatine fenestræ large.
									×	×	Skull not elevated.
×	×	×	×	×	×		×	×	×	?	Auditory meatus a notch.
								?		×	Pterygoid not extended above ectopterygoid.
								?	\	×	Palatines not meeting transverse.

Accordingly I propose to regard these genera (*Promystriosuchus, Angistorhinus,* and *Angistorhinopsis*) as an independent branch or subfamily of the Phytosauridæ. They may be known as the ANGISTORHININÆ.

The second subfamily here proposed, the PHYTOSAURINÆ, includes the genera *Paleorhinus, Brachysuchus, Leptosuchus, Phytosaurus, Clepsysaurus, Machaeroprosopus, Mystriosuchus,* and *Rutiodon.* Its distinguishing characters are: elongate compressed nares, the outward aspect of the orbits, and the short interpterygoid vacuity. Some genera in this subfamily develop rostral crests, a mid-dorsal premaxillary hump, a narrow palatal vault, posteriorly placed nares, and an extremely heterodont dentition.

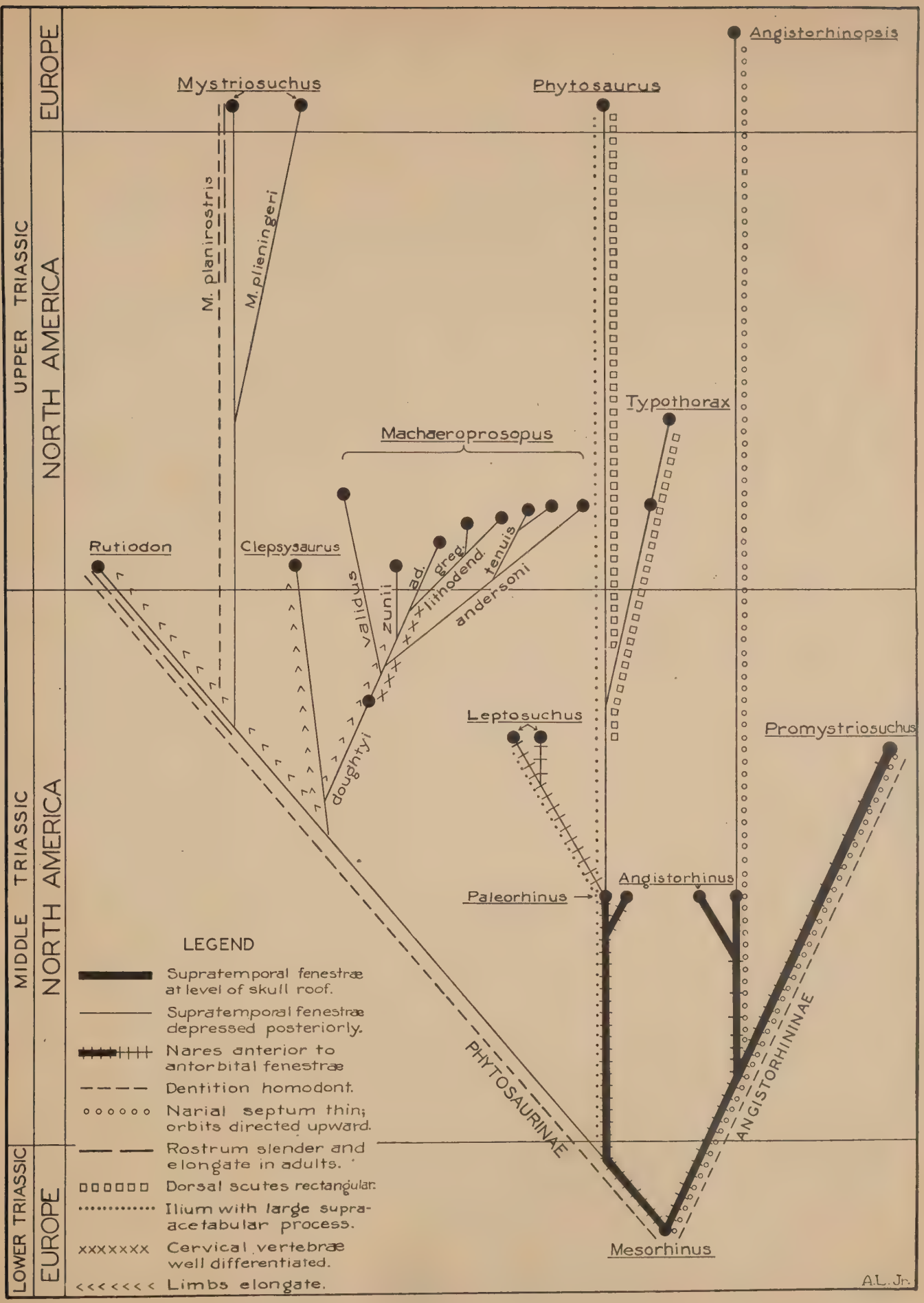

Fig. 49. Phylogeny of the known genera of the family Phytosauridæ.

In each subfamily some genera and species develop, doubtless independently, slender, elongate rostra, elongate squamosals, large posttemporal fenestræ, elevated skulls, broadened posterior processes of the ectopterygoids, small and vestigial post-palatine fenestræ, and depressed supratemporal fenestræ.

The "primitive" character of the supposed dermal scutes of *Phytosaurus* is a matter of doubt. These aëtosaur-like scutes may not actually be associated with *Phytosaurus* or they may be secondarily developed in this genus. By analogy with other reptiles I should not regard them as primitive.

Relations of *Phytosaurus* to *Leptosuchus* and *Paleorhinus* are suggested by the enlarged supra-acetabular process on the ilia of the three genera. But this evidence is weak because of lack of definite associations of skull and ilium in the three forms. Detailed evidences of relationships of other genera have been previously given. I submit then the foregoing tentative diagram (fig. 49) of the phylogeny of the Phytosauridæ.[12]

ADAPTIVE RADIATION IN PHYTOSAURS

What can be said concerning adaptive radiation in the phytosaurs? The most striking differences in the group are concerned with the proportions of the rostrum and the differentiation of the teeth. It is perhaps not idle to suggest a parallel with the modern crocodiles and gharials where there are adaptive forms developed independently in various groups. The smaller, long-snouted *Tomistoma* and *Gavialis* are fish-catchers while some of the huge, broader snouted Crocodilia are carnivores which prey upon terrestrial mammals.

There seems no good reason to regard the slender- and stout-snouted phytosaurs as separate groups and it is more consonant with the structural evidence to regard them as adaptive, polyphyletic series.

Coprolitic evidence as to the food of *Machaeroprosopus* has so far been negative. No fish scales have been found in numerous coprolites examined but Cope has found them in coprolites supposed to be of *Typothorax*. It seems likely that the young slender-snouted *Machaeroprosopus* were fish-catchers and that the adults preyed upon the stegocephalians whose remains are so numerous wherever the phytosaur bones are found. Numerous remains of small *Ceratodus*-like fishes are found in association with phytosaur remains in the Chinle.

There is considerable data showing that *Phytosaurus* and *Machaeroprosopus* were more highly terrestrial forms than *Mystriosuchus*. In Phytosaurus a process is developed above the acetabulum for the tendon of origin of the extensor iliotibialis muscle which occupies this position in the alligator. This would surely indicate a more powerful walking mechanism. More uncertain evidence is the specialization of the dermal armature in forms supposed to belong to *Phytosaurus*, and in *Typothorax*.

In *Machaeroprosopus* the dilatation of the pubis, the elongation of the limbs, the form of the scapula, and the development of the femoral trochanters and

[12] In this diagram *Brachysuchus*, recently described by Case, may occupy a position between *Paleorhinus* and *Leptosuchus*.

other features point to more advanced terrestrial habits than are seen in *Mystriosuchus* and *Rutiodon*.

In *Mystriosuchus* the great elongation of the caudal spines indicates a very highly compressed, swimming tail. So, in the European genera there appears to be a greater divergence between terrestrial and aquatic forms than in America.

RELATIONSHIPS OF PHYTOSAURS TO OTHER REPTILES

Huene, McGregor, and others have critically compared the skeleton and external skull characters of the phytosaurs and other reptiles. These authors essentially agree that the phytosaurs are closer to the aëtosaurs than to the crocodilians. Huene, Williston, and others have grouped the aëtosaurs with the Phytosauria and Pelycosimia, in the order or suborder Parasuchia. The crocodiles, dinosaurs, and pterosaurs are allied, all being placed by Williston in the superorder Archosauria.

The characters of the brain case and inner narial region have not yet been sufficiently studied in all these groups to allow an adequate check to be made from this highly conservative region of the skull. Watson (1916) has outlined results of his own studies of *Erythrosuchus*, "*Belodon*," *Plateosaurus*, *Iguanodon*, and the crocodiles and states that the following characters are found in combination in these genera, and indicate their affinity:

1. The separation of the inner ear from the brain cavity by bone.
2. The excessive narrowness of the cranial cavity between the ears.
3. The antero-posterior compression of the paroccipital process and the opening of the fenestra ovalis and the ductus fallopii on its ventral surface.
4. The enclosure of the anterior part of the brain by the bones usually but incorrectly called alisphenoids (=laterosphenoids) in crocodiles.

Lack of available specimens and published studies of the brain case of the pseudosuchians and pelycosimians prevents us from making adequate comparisons with these groups. I should therefore be content to follow the views of Huene and of Watson as far as they have gone. But it might be added that the ductus fallopii of Watson (=foramen for nerve VII) does not reach the paroccipital at any part of its course, in *Machaeroprosopus* and in *Erythrosuchus*. It leaves the skull in the paroccipital process of the proötic, near the anterior margin of the inner end of the paroccipital. Also, the fenestra ovalis lies not on the compressed paroccipital process but on the ventral surface of the base of the paroccipital in phytosaurs. Then too, the inner ear is widely exposed to the brain cavity according to Huene (1911*a*, fig. 2*d*) in *Erythrosuchus*. Furthermore, enclosure of the anterior portion of the olfactory tract is much less complete in crocodiles than in *Machaeroprosopus*.

After pointing out a number of important resemblances between the *Erythrosuchus* and the phytosaurs, Huene (p. 27) says:

> Der Vomer zeigt gewisse Abweichungen von den Phytosauriern, idem er zwar auch direkt von dem Pterygoid liezt und die Scheidewand Zwischen den choanen bildet, aber seine grössere Fläche sich hinter statt vor den Choanen befindet und indem er nicht von den Rändem der Maxilla und Praemaxilla unten bedeckt wird.

Huene evidently based this statement upon McGregor's study of the palate of *Mystriosuchus planirostris* as well as upon his own examinations of *M. plieningeri*. Unless *Machaeroprosopus* differs fundamentally from other phytosaurs in respect to the palatal aspect of the prevomer, these observations are incorrect. The relations of the prevomer in *Machaeroprosopus* are almost exactly as Huene has described them in *Erythrosuchus*. The prevomer forms the outer and lower borders of the choanal septum, but it extends posterior to the choanæ in an extensive plate, is bordered below, by the maxillæ and premaxillæ, anterior to the choanæ, and has no extensive surface anterior to the choanæ.

The limbs of *Erythrosuchus* were stouter, the humerus and femur being more like those of some cotylosaurs and pelycosaurs than like phytosaurs. These bones evidently terminated in very thick cartilaginous "epiphyses," which were not present in phytosaurs. This difference, if it appears in other pelycosimians, would seem of sufficient value to separate the suborder Pelycosimia from the Phytosauria.

The brain of *Erythrosuchus*, if we may judge from the relations of the pineal foramen and the foramen magnum, probably had a vertical flexure as in phytosaurs and saurischians.

Certain peculiarities of the brain case are held in common by the Saurischia and the Phytosauria. Of these the following in combination may be regarded as indicative of relationship rather than of retention of primitive characters in common:

1. Dorsal flexure of the mid-brain, with corresponding horizontal flexure of the cerebrum and olfactory region.
2. Presence of post-epiphyseal pockets in the brain case.
3. Presence of anterior processes in the cerebral region.
4. Extension of laterosphenoids anteriorly around olfactory tract.
5. Reduction of the internal auditory meatus.
6. Hypophysis vertical.
7. Epiphysis enlarged but without complete parietal foramen.
8. External apertures of cranial foramina not enclosed in ducts.

The crocodilia differ from the Phytosauria and Saurischia in points 1, 2, 3, 6, 7, and 8.
Most of the Permian reptiles differ from the Phytosauria and Saurischia in 1, 2, 4, 5, and 7.
The Ornithischia differ from the Saurischia and Phytosauria only in points 1, 2, and 3.

To the definition of the Phytosauria may now be added: tabulars fused or partly fused with parietals; interparietal fused or partly fused with supraoccipital; parietal foramen vestigial or absent; pterygoids extending into choanal septum; prevomers (=vomers) with dorsal, post-choanal laminæ and post-choanal palatal plates as in primitive reptiles; brain case with a pronounced dorsal flexure, a basal cavity for the pons varolii, and a complete bony canal for the olfactory tract and olfactory bulbs; laterosphenoids extensive antero-posteriorly and forming an incomplete, bony, interorbital septum; coronoids present.

In conclusion, I should confirm Huene's association of the Phytosauria with the Pelycosimia and should add that certain peculiar cranial characters of the Dinosauria (particularly the Saurischia) seem to show that the Phytosauria have closer affinities with them than with the Crocodilia.

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EXPLANATION OF PLATES

PLATE I

Machaeroprosopus adamanensis, type skull, 7038/26699, U. C. Mus. Pal., ×1/6.
J. L. Ridgeway, del.

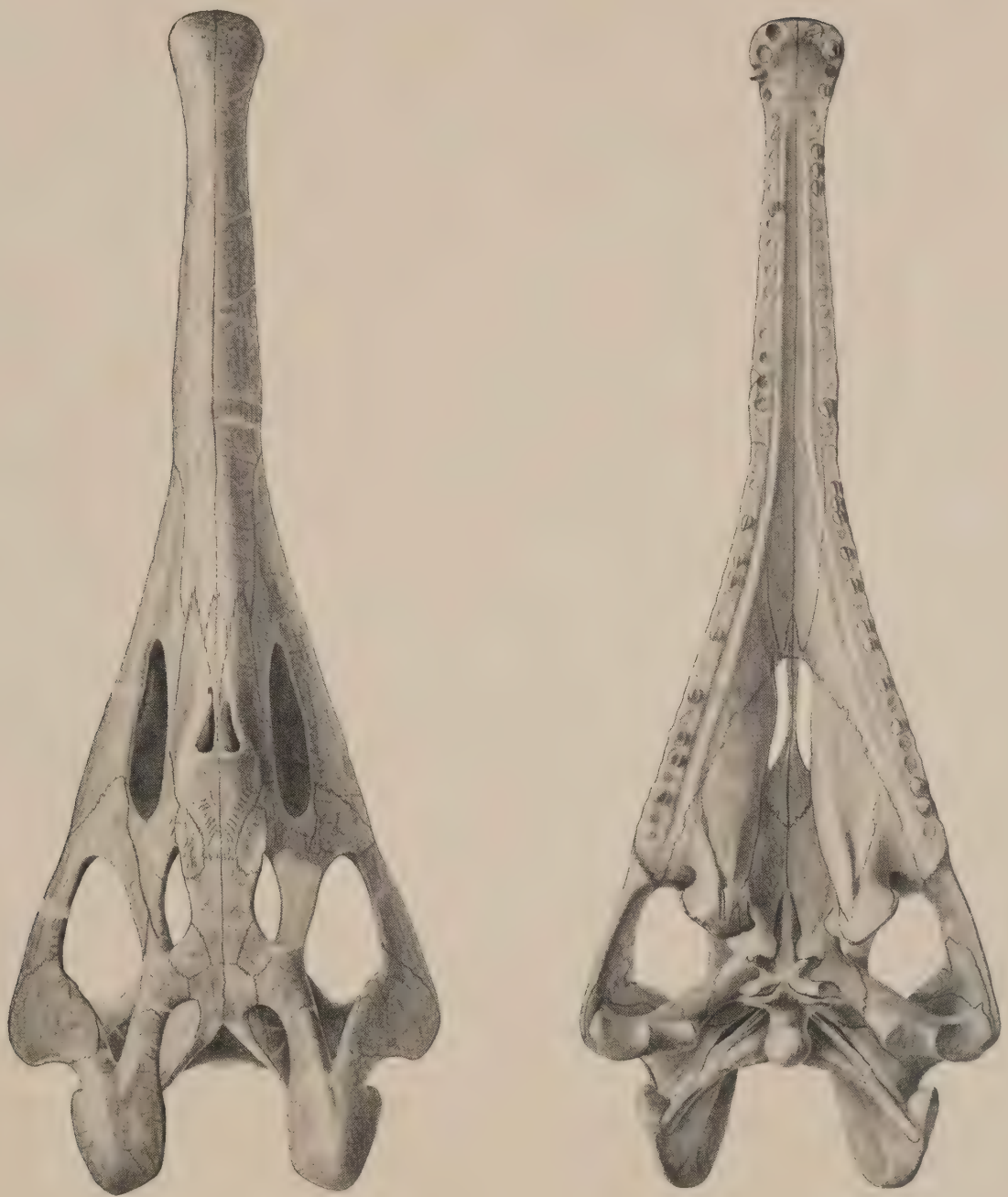
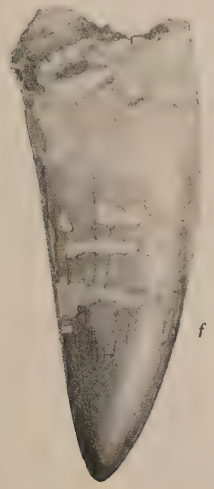


PLATE II

a–e, M. adamanensis, type skull. *a.* Lateral view of skull and lower jaws, ×1/6. *b.* Second left premaxillary tooth, lingual view, ×1. *c.* Fifth and seventh anterior left maxillary teeth, buccal view, ×1. *d.* Fourteenth left maxillary tooth, ×1. *e.* Posterior view of skull, ×1/6. *f. Machaeroprosopus* sp.?, first left premaxillary tooth, lingual view, ×1. *a* and *e* drawn by J. L. Ridgeway; *b–d,* and *f* by Helen Rearwin.

a



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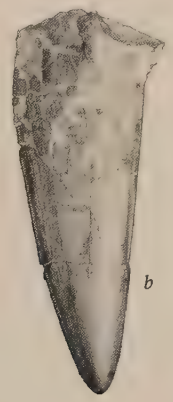

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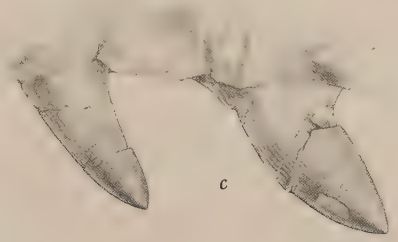

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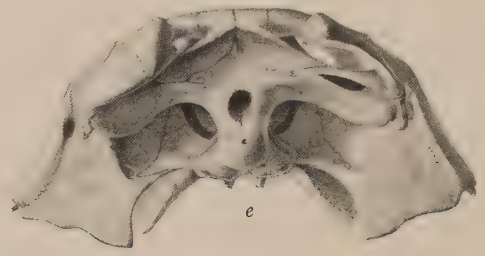
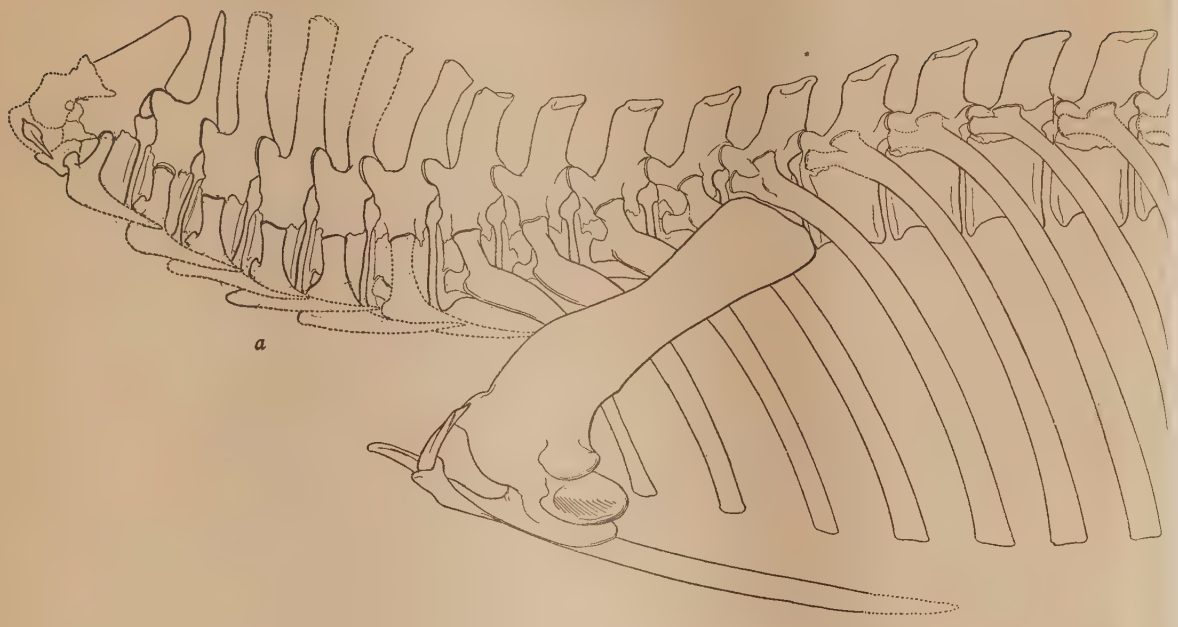


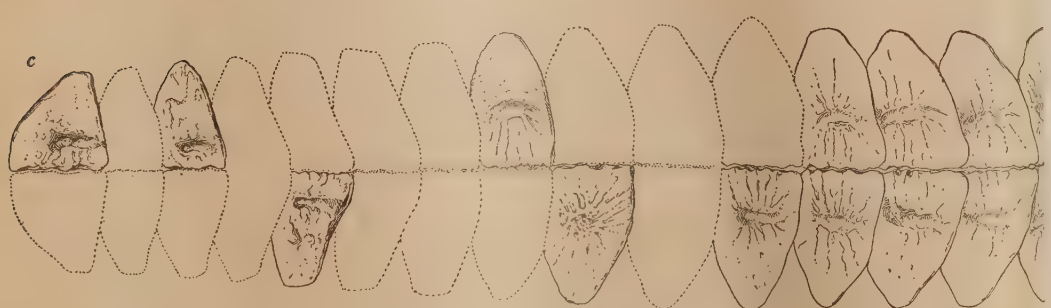
e

PLATE III

Machaeroprosopus adamanensis (type), 7038/26699, U. C. Mus. Pal., parts of axial skeleton and dermal scutes, ×1/9. *a*. Vertebral column, from atlas to third caudal; ribs and girdles, from left side. *b*. Column from axis to third caudal. *c*. Mid-dorsal series of dermal scutes; those opposite the 13–15 and the 17–23 vertebræ were found in place adjoining the spines of those vertebræ.


a

b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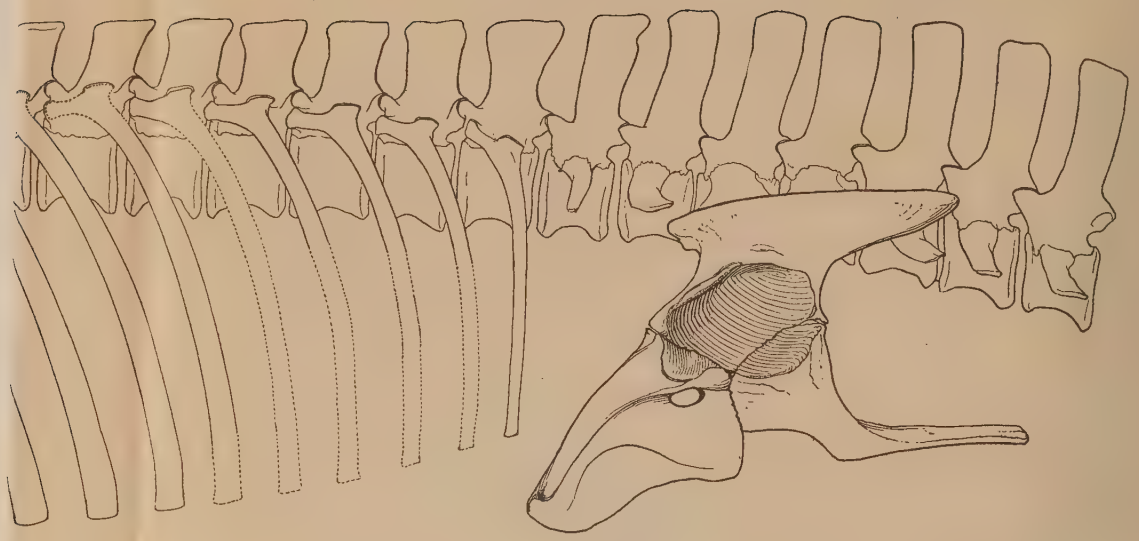
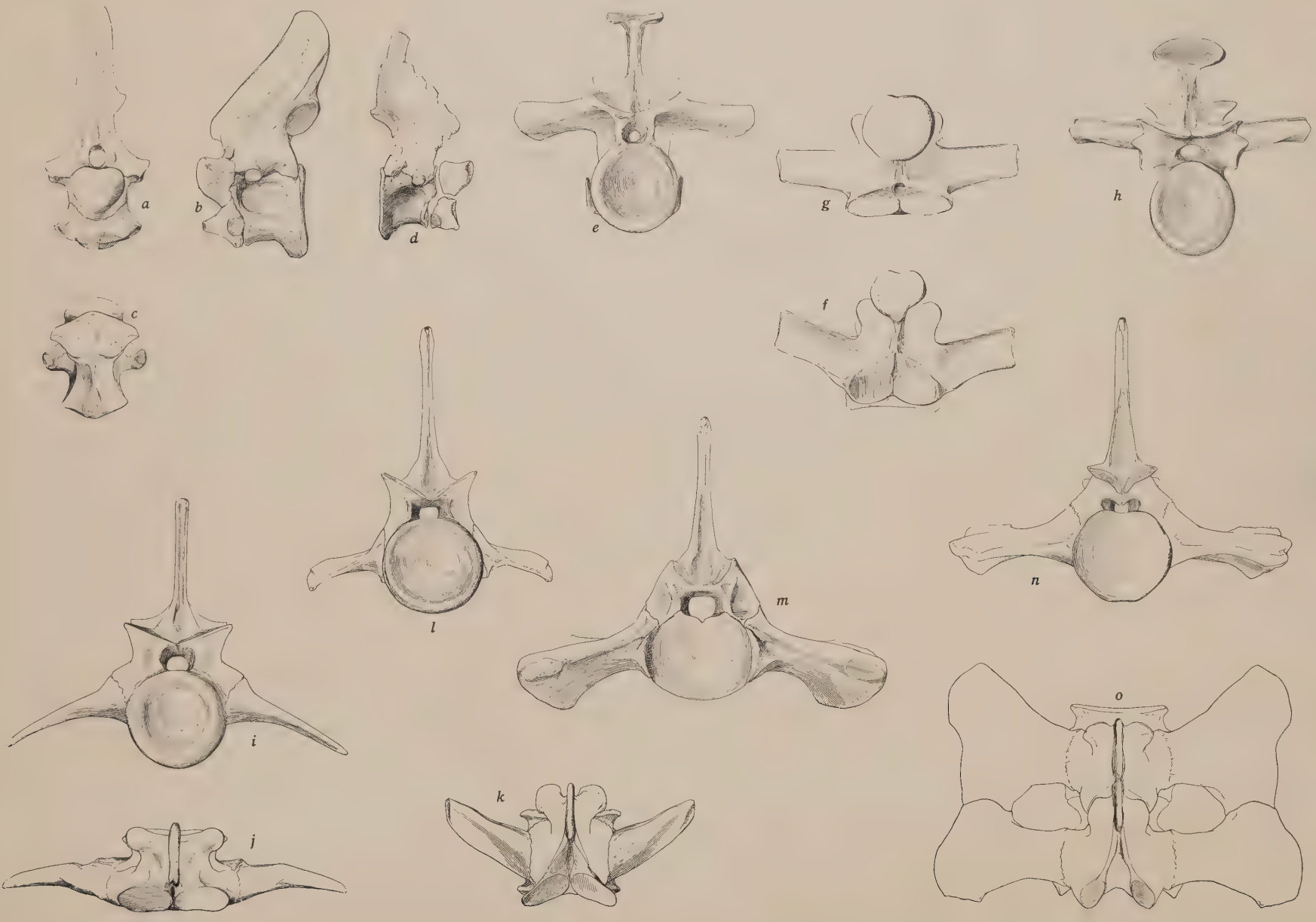


PLATE IV

Machaeroprosopus adamanensis type specimen (except *d*), 7038/26699, vertebræ, ×¼. *a–c*. Axis, anterior left and ventral views. *d*. Axis of a young specimen (7046/27025), right side, showing dissociated odontoid and intercentrum. *e–f*. Tenth vertebra (=third thoracic), anterior and dorsal views. *g–h*. Thirteenth vertebra (=sixth thoracic), anterior and dorsal views. *i–j*. Twenty-fourth (=first lumbar), anterior and dorsal views. *k–l*. Twenty-eighth (=first caudal), anterior and dorsal views. *m*. First sacral, anterior view. *n*. Second sacral, posterior view. *o*. Sacrum, dorsal view.


a
b
d
e
g
h
c
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l
m
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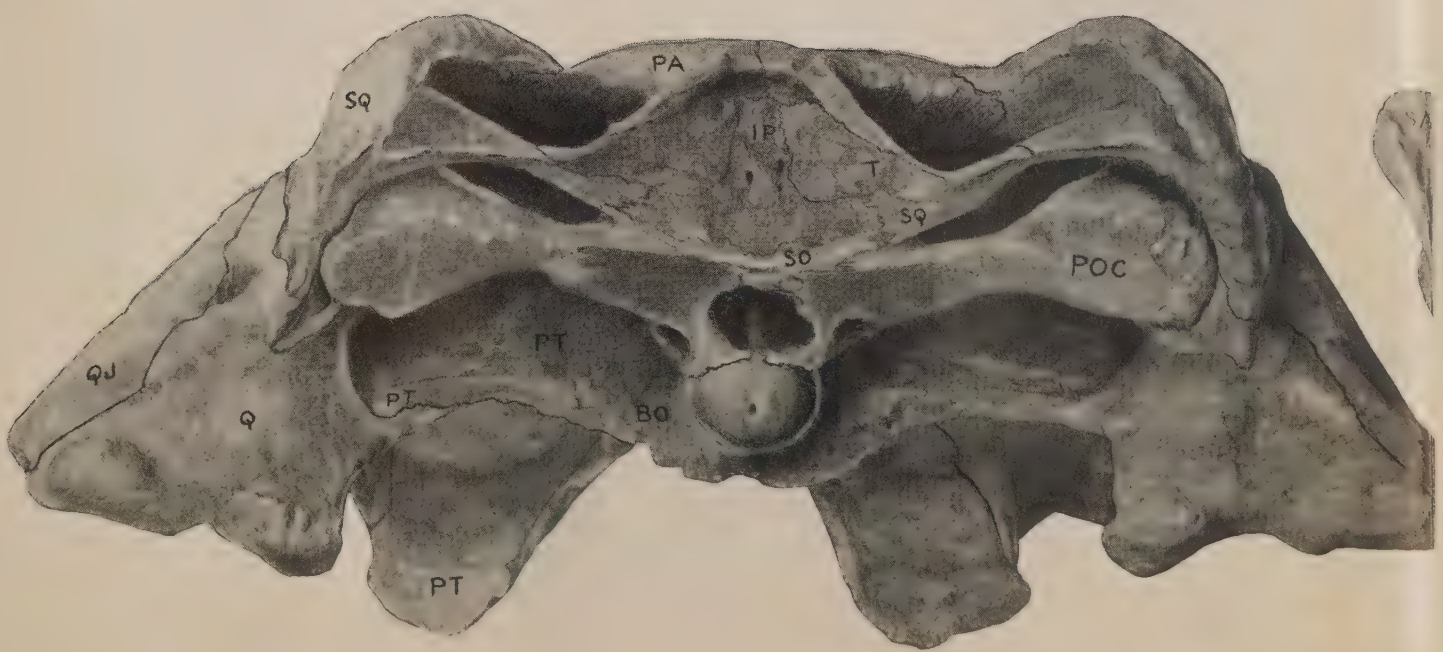
i
o
k
j

PLATE V

Machaeroprosopus gregorii type specimen, A270/27200, U. C. Mus. Pal., ×1/3.
From photographs by W. C. Matthews.

SQ
Q
QJ
SA
AN
D


PA
SQ
IP
T
SQ
SO
POC
PT
QJ
PT
Q
BO
PT

ART
AN

PLATE VI

Machaeroprosopus gregorii type specimen, A270/27200, U. C. Mus. Pal., ×1/3.
From photographs by W. C. Matthews.

PX
MX
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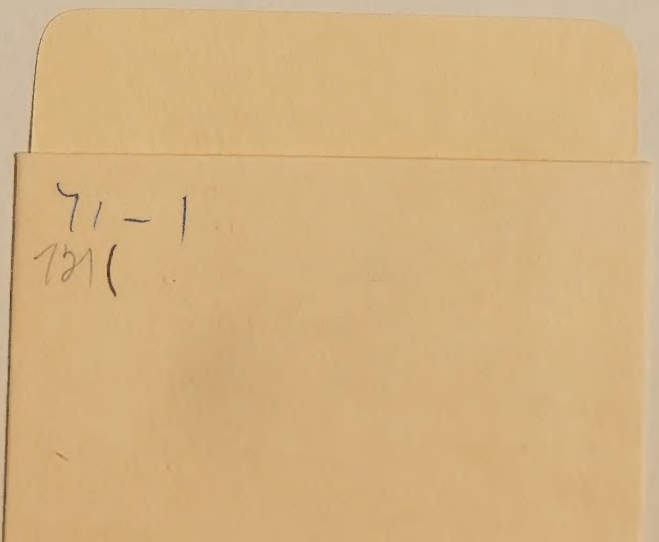
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C15
V.10